Copyright Statement

The digital copy of this thesis is protected by the Copyright Act 1994 (New Zealand).

This thesis may be consulted by you, provided you comply with the provisions of the Act and the following conditions of use:

- you will use the copy only for the purposes of research or private study
- you will recognise the author's right to be identified as the author of the thesis and due acknowledgement will be made to the author where appropriate
- you will obtain the author's permission before publishing any material from the thesis.
INTRASEXUAL TERRITORIALITY AND THE
SPATIAL AND SOCIAL BEHAVIOUR OF CAPTIVE
FERAL FERRETS (*Mustela furo* L., Carnivora:
Mustelidae).

--------------------------------------------------------

A thesis
submitted in partial fulfilment of the requirements for the degree of
Doctor of Philosophy

at
Lincoln University
Canterbury, New Zealand

by
Gonzalo Medina-Vogel

1998
This thesis is dedicated to M. Ximena Henzi G.
ABSTRACT

Abstract of a thesis submitted in partial fulfilment of the requirements for degree of Doctor of Philosophy at Lincoln University, New Zealand.

INTRASEXUAL TERRITORIALITY AND THE SPATIAL AND SOCIAL BEHAVIOUR OF CAPTIVE FERAL FERRETS (Mustela furo L., Carnivora: Mustelidae).

by

Gonzalo Medina-Vogel

I observed eight male and five female feral ferrets (Mustela furo) directly and by video camera in a 36 m² outdoor enclosure equipped with six dens and 13 tunnels. Five (Replicate I) and six (Replicate II) social groups were observed at three levels of food availability. I determined their main range and core area sizes, use intensity of dens and core areas, and the extent of spatial and temporal overlap between individuals. I assessed the effect of sex, grouping, density, social status and observation period on these activities. I also determined the effect of food availability on main range and core area sizes, use intensity of the arena, dens and core areas, spatial and temporal overlap and social status. The ferrets were observed in both mating and non-mating periods and these data were compared. I also determined the effect of food availability, mating period, social status, density and group
composition on the ferrets' behaviour and daily activity levels.

The spatial patterns observed were consistent with previous studies of free-ranging feral ferrets in New Zealand. Males and female main ranges were similar. Main range size increased with increasing ferret density, and their core area use intensity decreased. Dominant males overlapped more in both space and time with females than did subordinate males. There was less den sharing between members of the same sex than between sexes. These observations are consistent with the hypothesis that intrasexual territoriality occurs among wild ferrets.

When food was restricted, males' main range size and core area use intensity both decreased. Main range and core area overlap reduced but use intensity of the overlapped areas increased. This reduction in main range size at reduced food availability was most evident when ferret density was high. Restricting food also caused the overlap in main range areas of males and females to reduce and their den temporal overlap to increase. However, changes in food availability had no effect on the relationship between spatial activity and ferrets' social status. I concluded that avoidance to reduce intraspecific competition, may be the factor that induces increased dispersion of carnivores during periods of food scarcity.

During the mating period both male and female ferrets increased their main ranges and reduced their denning time. Dominant males increased their overlap with females and their exclusion of subordinate males from their main ranges, core areas and dens. During the mating period female spatial behaviour influenced the territorial behaviour of males.

During the non-mating period ferrets spent 86% of their time resting, 6% foraging and 3% vigilant. Dominant males rested more than did subordinate males. Ferrets with food in excess of their maintenance requirement spent more time resting than did ferrets with maintenance food or no food. Females rested less, interacted less and mated more than did
males. Dominant males rested less, marked more and mated more than subordinate male ferrets.

Based on these findings, I propose a model for variation in home range, territoriality and dispersion of solitary, sexually dimorphic carnivores in relation to changes in prey abundance. I predict that for small intrasexual territorial carnivores, males will progressively reduce their home range and reduce their intrasexual territoriality as prey availability increases from a 'low' and a 'high' threshold; between these thresholds females will show little variation in their home range sizes and intrasexual territoriality. Below the low and above the high thresholds, intrasexual territoriality will break down and the spatial structure of the population will be indeterminate.

The hypotheses and predictions raised by this study must be tested with ferret populations in the field. Nevertheless, according to the predictions of this study predicts that the outcomes of feral ferret control operations in New Zealand will differ depending on the reproductive status of the population. Therefore, control operations could be most effective in the non-mating period when reproductive females are more socially dominant. Finally, I conclude that in order to help in the understanding of the social and behaviour ecology of small carnivores, the described methodology is an effective means of studying in captivity aspects of ferret social organisation and behaviour that would be very difficult to observe in free-ranging animals, provided the findings can be validated by subsequent research on free ranging animals under natural conditions.
ACKNOWLEDGMENTS

I thank my joint supervisors Drs. G. J. Hickling, B. K. Clapperton and R. R. Scott for their interest and support throughout this project. In particular, I wish to acknowledge the useful discussions I have had with them, their suggestions and constructive criticism of the research manuscripts, and for the faith they showed in allowing me considerable latitude to explore my own ideas. I also take this opportunity to acknowledge the Ecology and Entomology Group, Lincoln University, for providing research facilities and funding.

I also express my gratitude to, and acknowledge the assistance of, Norman and Marion Moe during my ferret trapping fieldwork. I am grateful to the Blackburn family for their help and friendship.

Dr. Chris Frampton provided excellent statistical advice.

I am grateful to the New Zealand Ministry of Foreign Affairs and Trade, for the NZODA Postgraduate Full Scholarship that supported my studies.

I would also thank the Instituto de Ecología y Evolución, and Facultad de Ciencias of the Universidad Austral de Chile for supporting my overseas postgraduate studies.

Finally I am indebted to my family: Ximena, Sofía, Isabel, Amy, and my parents, Mrs Harda Vogel B. and Fernando Medina R. for their faith, love, encouragement, guidance, financial and emotional support without which this work was not possible. I am sad that my father did not live to see me complete this research and my PhD.
PREFACE

Chapters 3, 4, and 5 of this thesis represent a compilation of three different manuscripts that have been formatted according to the style of the journals where these are to be submitted. The more general material in Chapters 1, 2, 6 is presented in the format specified by "Notes on the preparation of Theses and Dissertations" (Lincoln University Library Paper No. 16).
# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>-section</th>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Abstract</td>
<td>i</td>
</tr>
<tr>
<td></td>
<td>Acknowledgments</td>
<td>iv</td>
</tr>
<tr>
<td></td>
<td>Preface</td>
<td>v</td>
</tr>
<tr>
<td></td>
<td>Table of contents</td>
<td>vi</td>
</tr>
<tr>
<td></td>
<td>List of tables</td>
<td>xi</td>
</tr>
<tr>
<td></td>
<td>List of figures</td>
<td>xii</td>
</tr>
<tr>
<td></td>
<td>Chapter one: Introduction</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1.1 Background</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1.2 Thesis justification</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>1.3 Thesis aim</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>1.4 Thesis objectives</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Chapter two: Literature review</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>2.1 Background</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>2.2 Intraspecific variation in mustelid spacing patterns and social behaviour</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>2.2.1 Martens and fishers</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>2.2.2 Weasels</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>2.2.3 Ferrets and polecats</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>2.2.4 Mink</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>2.2.5 Variation in mustelid territoriality</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>2.3 Implications of field data for theory</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>2.4 Implications for management of small carnivores</td>
<td>24</td>
</tr>
</tbody>
</table>
Chapter three: Assessing spatial activity in captive feral ferrets, *Mustela furo* L.

(Carnivora: Mustelidae) ........................................................................................................ 26

3.1 Abstract ......................................................................................................................... 26
3.2 Introduction .................................................................................................................... 27
3.3 Methods ......................................................................................................................... 28
  3.3.1 Outdoor enclosure ...................................................................................................... 28
  3.3.2 General procedures ................................................................................................... 30
  3.3.3 Size of main range and core area ............................................................................. 31
  3.3.4 Use intensity ............................................................................................................. 32
  3.3.5 Intrasexual territoriality ......................................................................................... 32
  3.3.6 Social status ............................................................................................................. 33
  3.3.7 Statistical analysis .................................................................................................... 33
3.4 Results ............................................................................................................................ 34
  3.4.1 Size of main range, core area and den use intensity .............................................. 35
  3.4.2 Spatial overlap ......................................................................................................... 34
  3.4.3 Use intensity overlap of main range, core area and dens ...................................... 35
  3.4.4 Temporal overlap of arena and dens ...................................................................... 39
  3.4.5 Effect of observation period ................................................................................... 40
3.5 Discussion ....................................................................................................................... 43
  3.5.1 Spatial activity ......................................................................................................... 43
  3.5.2 A critique of this captive-animal methodology ....................................................... 45
  3.5.3 Acknowledgments .................................................................................................... 47
3.6 References ...................................................................................................................... 47
Chapter four: Spatial activity of captive feral ferrets (*Mustela furo* L.) I: the

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>effect of food availability and the mating period</td>
<td>51</td>
</tr>
<tr>
<td>4.1 Abstract</td>
<td>51</td>
</tr>
<tr>
<td>4.2 Introduction</td>
<td>52</td>
</tr>
<tr>
<td>4.3 Methods</td>
<td>54</td>
</tr>
<tr>
<td>4.3.1 Outdoor enclosure</td>
<td>54</td>
</tr>
<tr>
<td>4.3.2 General procedures</td>
<td>55</td>
</tr>
<tr>
<td>4.3.3 Space use intensity</td>
<td>56</td>
</tr>
<tr>
<td>4.3.4 Intrasexual territoriality</td>
<td>57</td>
</tr>
<tr>
<td>4.3.5 Statistical analysis</td>
<td>58</td>
</tr>
<tr>
<td>4.4 Results</td>
<td>59</td>
</tr>
<tr>
<td>4.4.1 Effect of food availability</td>
<td>59</td>
</tr>
<tr>
<td>a.- Main range size and area overlap</td>
<td>59</td>
</tr>
<tr>
<td>b.- Intrasexual territoriality and differences between the ferret sub-</td>
<td></td>
</tr>
<tr>
<td>groups</td>
<td></td>
</tr>
<tr>
<td>4.4.2 The effect of the mating period</td>
<td>61</td>
</tr>
<tr>
<td>a.- Main range size, core area size, use, and dens use intensity</td>
<td>61</td>
</tr>
<tr>
<td>b.- Intrasexual territoriality and differences between the ferret sub-</td>
<td></td>
</tr>
<tr>
<td>groups</td>
<td>62</td>
</tr>
<tr>
<td>4.5 Discussion</td>
<td>69</td>
</tr>
<tr>
<td>4.5.1 Effect of food on ferrets' spatial activity</td>
<td>69</td>
</tr>
<tr>
<td>4.5.2 Effect of the mating period on ferrets' spatial activity</td>
<td>70</td>
</tr>
<tr>
<td>4.5.3 Variation in captive feral ferrets' intrasexual territoriality</td>
<td>72</td>
</tr>
<tr>
<td>4.5.4 Intrasexual territoriality and females' tactics</td>
<td>76</td>
</tr>
</tbody>
</table>
Chapter five: The effect of food availability and mating period on the behaviour and activity levels of captive feral ferrets (*Mustela furo* L.)

5.1 Abstract .................................................. 84
5.2 Introduction .............................................. 85
5.3 Methods ................................................... 87
  5.3.1 Outdoor enclosure ................................. 87
  6.3.2 General procedures ............................... 87
  6.3.3 Behaviour and activity level ................... 88
  6.3.4 Statistical analysis ............................... 89
5.4 Results ................................................... 90
  5.4.1 Time budgets ....................................... 90
  5.4.2 Activity levels ...................................... 91
5.5 Discussion ................................................ 96
  5.5.1 Time budgets ....................................... 96
  5.5.2 Activity levels ...................................... 97
  5.5.3 Acknowledgments .................................. 99
5.6 References ............................................... 99

Chapter six: .................................................... 102
6.1 General discussion ..................................... 102
  6.1.1 Spatial organisation of New Zealand feral ferrets ....................................... 102
  6.1.2 Wild studies *versus* captive studies ....................................................... 104
6.1.3 Models of intrasexual territoriality ...................................................... 106

a. Powell’s model ..................................................................................... 106

b. Refinements to the model .................................................................. 106

c. The effect of the mating period .......................................................... 108

d. The model’s predictions .................................................................. 108

6.1.4 Management implications ............................................................... 109

6.2 Specific conclusions ........................................................................ 111

6.3 References ........................................................................................ 114
LIST OF TABLES

TABLE                        PAGE

Chapter two

1. Home range size and percentage of overlap within and between sexes of 22 weasels, polecats, ferrets, mink, martens and fishers............................... 22

Chapter three

1. Effect of ferret sub-group composition on use intensity overlap of dens and the area overlap of main ranges and core areas.................................................. 41

2. Effect of male ferrets' sub-group composition on temporal overlap in the arena and dens................................................................................................. 42

Chapter four

1. Effect of food availability on the area overlap of ferret main ranges for the various different ferret sub-groups................................................................. 61

2. Effect of social status of eight male ferrets on overlap with five females during non-mating and mating periods................................................................. 66

3. Differences in temporal overlap of arena and dens between the non-mating and mating periods for two females (FF), two females and one male (FFM), one female and one male (FM), two males and one female (MMF), two males (MM) and three males (MMM)................................................................. 67

Chapter five

1. Comparison of the activity level (expressed as proportions of time observed) of three sub-groups of ferrets during the non-mating and mating periods............... 95
# LIST OF FIGURES

## Chapter three

1. Sketch of (a) the grid for determination of space use, (b) the outdoor enclosure and (c) a separate ferret cage, tunnel and den. All measurements are in metres.  
   ![Image](image1.png)  
   **Page 29**

2. Log-transformed frequency of cell use \[ \log \left( \sum \frac{\text{cells used}}{30} + 1 \right) \] plotted against proportional use of each grid cell (pooled data for six different ferret social grouping). The first value between higher values (at 3.0; see arrows) was used to define ‘core area’ (adapted from Harris et al. 1990).  
   ![Image](image2.png)  
   **Page 36**

3. Mean size of main ranges of eight male and five female ferrets in various combinations in the two replicated experiments.  
   ![Image](image3.png)  
   **Page 37**

4. Effect of number of ferrets on size of individual ferrets’ main ranges and use intensity of core areas (replicates I and II combined).  
   ![Image](image4.png)  
   **Page 38**

5. Effect of sub-group composition on main range overlap for five females and eight males (Replicate combined).  
   ![Image](image5.png)  
   **Page 39**

6. Influence of observation period length on the estimate size of the ferrets’ main range.  
   ![Image](image6.png)  
   **Page 40**

## Chapter four

1. Effect of food availability on main range size of eight male and five female ferrets. Within each sex, bars with different letters indicate means that differ significantly (Fisher’s LSD: \( P<0.05 \)).  
   ![Image](image7.png)  
   **Page 60**

2. Mean size of main range of eight male and five female ferrets in the non-mating and mating periods in two replicate experiments combined.  
   ![Image](image8.png)  
   **Page 63**
3. Den use intensity by eight male and five female ferrets in the non-mating and mating periods in two replicate experiments............................................................... 64

4. Differences between three dominant and five subordinate male ferret's mean size of main range in the non-mating and mating periods in two replicate experiments........................................................................................................... 65

5. Mean area overlap between main range of eight male and five female (FM) ferrets and common area overlap between five males combined in sub-groups of three males (MMM) in the non-mating and mating periods........................................... 68

6. Proposed model of variation in intrasexual territoriality among solitary, sexual dimorphic carnivores during the non-mating period. Bold arrows indicate direction of the increase. Between the two thresholds there is little variation in females' home range size and territoriality.......................................................... 75

Chapter five

1. Arcsin-transformed proportions of time (excluding resting) spent by eight male and five female ferrets during the a) non-mating and b) mating periods............... 92

2. Variation of the arcsin-transformed proportions of time (excluding resting) of eight male and five female ferrets at three food levels (DFM: double food maintenance, FM: food maintenance and NF: no food) during the a) non-mating and b) mating periods................................................................. 93

3. Activity level of eight males and five female ferrets during the a) non-mating and b) mating periods........................................................................................................ 94
CHAPTER ONE

INTRODUCTION

1.1 Background

The ferret (*Mustela furo* L.) is a small carnivore (0.4 -1.85 kg) of the family Mustelidae. Ferrets were introduced to New Zealand in the early 1880s to control rabbit (*Oryctolagus cuniculus* L.) populations (Lavers & Clapperton 1990). By the turn of the century, ferrets were well established and had begun to have an adverse impact on native fauna. Despite ferret control campaigns that began in the 1930s, New Zealand now has the largest known population of feral ferrets (Lavers & Clapperton 1990). Ferrets have been recently implicated in the decline of a number of threatened endemic bird species (Murphy 1996), and as a possible vector of bovine tuberculosis (Tb; *Mycobacterium bovis*) to domestic livestock (Ragg & Walker 1996). Relatively little is known about ferret ecology, movements and social behaviour in New Zealand, yet this information is critical in understanding the effect of ferrets in limiting rabbit numbers, their role in the epidemiology of Tb, and in designing effective predator control programmes (King & Moors 1979, Moller *et al.* 1996, Ragg in review a.). This lack of information is due, in part, to the difficulties and cost of studies to determine spatial patterns and behaviour of free-ranging mammals (Harris *et al.* 1990).

Members of the genus *Mustela* are typically described as solitary except for reproductive purposes (Powell 1979). Individuals may be transient (i.e., merely passing through an area), temporarily resident (staying a short time) or resident (staying for extended periods or for the duration of their lives). At the population level, there appears to be a well-structured pattern of spacing between individuals. Males and females share the same area, but will exclude others of the same sex. This system, termed “intrasexual territoriality” (Powell 1979), may be affected by variation in resource availability (Powell 1993). How intrasexual territoriality...
varies in response to changes in availability of resources such as food is not well understood and has been little studied (Powell 1993). However, there are some predictions and hypotheses about how variation in food availability and receptive females during the mating period might affect the social and spatial behaviour of small carnivores that exhibit intrasexual territoriality.

First, Erlinge & Sandell (1986) predicted shifts between territorial and non-territorial behaviour in a situation with stable resources if a species alternates between decisive resources. For example, if one resource is the critical factor during winter and the other critical during summer, and if the two resources have different spatial characteristics, then changes in relative importance of the resources with season should induce seasonal changes in the species' social organisation. They supported these predictions with their findings in male stoats' (*Mustela erminea* L.) social organisation in isolated marshes in southern Sweden. This marsh habitat held a dense populations of voles (*Microtus agrestis* L. and *Arvicola terrestris* L.) and was separated by dry grazed areas. Stoats were organised in an intrasexually territorial system during the non-mating period. The decisive resource during that period was food (i.e. the voles), which was concentrated within marsh patches that could be defended by individual stoats. During the mating period, however, the males' territorial system broke down and was replaced by a non-territorial pattern with greatly overlapping home ranges. Erlinge & Sandell (1986) concluded that the formation of these new spacing patterns was favoured by the spatial distribution and ephemeral nature of the limited number of females in oestrus during the mating season.

Second, Sandell (1989) predicted that one of the main characteristics of the spacing pattern in a carnivore population is the extent of range overlap between individuals. For ranges to be exclusive, the food resource must be so sufficiently evenly distributed and stable that the
range contains just enough to support an individual during the most critical period of the year. If the food resource varies in space and time, the range must be large enough to provide for the animal during the time when food is most scarce. Therefore, exclusive ranges are expected when food resources are stable and evenly distributed, whereas a system of overlapping ranges is expected when the timing and spacing of available food varies. Furthermore, exclusive ranges should be relatively smaller than overlapping ranges.

Females in non-cooperative species, like most small carnivores, must rear young by themselves, so their reproductive success is closely correlated with the amount of energy they can allocate to reproduction. Thus, for solitary female carnivores, food is the most important resource, so Sandell (1989) predicted that females should adopt a behavioural tactic that maximises their chances of securing food resources. Therefore, female range size should be correlated with food abundance during the most critical period of the year.

More recently, Powell (1993, 1994) proposed that some forest carnivores exhibit intrasexual territoriality because the distribution and availability of the most likely decisive resource for these species (food) allows a trade-off not possible for species with individual territories. This in turns allows male spacing to be affected by female spacing, as well as by the distribution of food. He showed that a male marten (*Martes americana* T.) with an intrasexual territory has a smaller probability of reproductive failure than does a male with an individual territory. However, he could not identify a benefit for females that sharing their territory with a male; he therefore hypothesised that intrasexual territoriality in small carnivores is imposed on females by males who are larger than, and thus dominant to, the females.
1.2 Thesis justification

Based on the Erlinge & Sandell (1986), Sandell (1989) and Powell (1993, 1994) hypotheses, it seems likely that the social structure and spatial behaviour of New Zealand feral ferrets varies between the non-mating and mating periods. If so, the outcomes of ferret control operations may depend on factors such as food availability, population density, social status and season. For example, in a control campaign the optimal spacing of bait stations will be determined by home range size. Variation in territoriality will influence home range size, so the spacing between bait stations will need to be changed in response to this. However, most aspects of behaviour and spatial patterns of wild ferrets are poorly known, with most observations of ferret and polecat (*Mustela putorius* L.) behaviour having been made on captive animals (e.g., Poole 1967, 1972, 1973; Biben 1982; Stockman *et al.* 1986; Clapperton *et al.* 1988, Clapperton 1989).

The few studies on free-ranging feral ferrets in New Zealand tend to be contradictory. A mark-recapture study at Pukepuke Lagoon (Moors & Lavers 1981) concluded that feral ferrets were exhibiting intrasexual territoriality and that home ranges of females overlapped considerably at one site when the abundance of prey (*mice, Mus musculus* L.) was high. In contrast, Ragg (in review a) concluded from a radio-tracking study supported by mark-recapture sessions of a high density ferret population near Palmerston, Otago, that the extensive overlap of home ranges between ferrets of the same sex did not support a model of intrasexual territoriality. Both Ragg (in review a) and Norbury *et al.* (in review) have suggested that ferrets have higher rates of social contact than do other solitary mustelid species, and that the different conclusions of the various studies undertaken to date may be attributed to variation in ferret density relative to prey density.
In this study of wild-caught ferrets held in an outdoor enclosure, I developed new observation techniques to study the mechanisms underlying ferret spatial patterns and behaviour. I experimentally tested predictions made by Erlinge & Sandell (1986), Sandell (1989) and Powell (1993, 1994) about variation in, and breakdown of, the intrasexual territoriality system in small carnivores in response to changes in food and mate availability. I compared my results with data from free-ranging feral ferrets and other carnivores to help support or reject these predictions and hypotheses. Based on these results, I then propose a refined model that aids in better understanding variation in intrasexual territoriality in small sexually dimorphic carnivores.

1.3 Thesis aim

The aim of the work reported in this thesis was to obtain information about the social and spatial behaviour of feral ferrets in a mid Canterbury lowland environment using an experimental captive-animal methodology. By comparing the results with other studies, I thereby aimed to obtain reliable data that would help support or reject predictions and hypotheses about the mechanisms underlying variations in the territorial system of small carnivores.

1.4 Thesis objectives

1. To develop an experimental technique to study the spatial and social behaviour of captive feral ferrets.

2. To determine if ferrets in captivity exhibit intrasexual territoriality.

3. To test how variation in food availability affects the social and spatial behaviour of ferrets in captivity.
4. To determine how the mating period affects the social and spatial behaviour of ferrets in captivity.

5. To determine whether the focus of males’ spatial behaviour switches between two different resources (food and females) during the mating period.

6. To test how variation in ferret density affects the social and spatial behaviour of ferrets in captivity.

7. To determine the activity budget of ferrets in captivity and how it is affected by the mating period.

8. Based on these results, to suggest ways in which the control of pest populations of feral ferrets in New Zealand could be enhanced.
CHAPTER TWO
LITERATURE REVIEW

2.1 Background

The family Mustelidae is divided into four subfamilies: Mustelinae (weasels, polecats, fishers, martens, wolverines and tayras), Mellivorinae (badgers), Mephitinae (skunks) and Lutrinae (otters). Mustelids are small to medium size carnivores (0.05 - 45 kg) with long bodies and short legs. Most species are solitary and live in forest habitats, although group living is found in European badgers (Meles meles L.), sea otters (Enhydra lutris L.) and giant otters (Pteronura brasiliensis G.) (Bekoff et al. 1984).

Most animals are territorial only when there is a decisive resource and when the cost of defence is less than the benefit accrued from territoriality (Brown 1964 cited by Krebs & Davies 1987). Territoriality, defined for small carnivores as an area of exclusive use (Powell 1979), may affect some individuals by limiting access to resources (e.g., food, mates) and influencing the extent of parental care (Krebs & Davies 1987). Hawley & Newby (1957) were the first to report intrasexual territoriality in mustelids, based on a live-trapping study of martens (Martes americana) in Glacier National Park, Montana. The home ranges of adult martens of both sexes were rather evenly distributed with little overlap, whereas martens of opposite sex appeared quite tolerant of each other. When an adult marten disappeared the territories of adjacent martens of the same sex extended into the vacant area. Transients and temporary residents did not affect the spacing patterns of resident martens. Subsequent contributions to the concept of intrasexual territoriality in mustelids from Erlinge & Sandell (1986), Sandell (1989) and Powell (1993, 1994) are summarised in Chapter one.

2.2 Intraspecific variation in mustelid spacing patterns and social behaviour

Data are available from studies on a range of mustelids species for testing predictions from the intrasexual territorial hypothesis of Powell (1993, 1994) and Erlinge & Sandell (1986).

2.2.1 Martens and fishers

Home range size and overlap estimates vary greatly within and between marten and fisher species. This variation is due in part to a lack of consistency in methods of calculating home range size, in part to the use of minimum convex polygon methods, that include much area not actually used by animals, and in part to true variation (Powell 1994). Most but not all Martes populations exhibit intrasexual territoriality. Powell (1994) found correlations
between intrasexual territoriality and pronounced sexual dimorphism in body size, elongate shape, and a high degree of carnivory. He also found that spacing behaviour varies across the species' range and through time.

Martens: female American marten vary their use of home range on a seasonal basis (Wyane & Sherburne 1984). Females' home range changed from June to August while that of males did not, possibly because of increased use of maternal dens and resting sites. As the kits reach independence, the females made greater use of relatively open sites in tree canopies (Wyane & Sherburne 1984).

Despite their greater energy needs, and contrary to predictions of Lindstedt et al. (1986) and Sandell (1986), Katnik et al. (1994) showed that in an American marten population in north-central Maine, females raising offspring occupied smaller ranges than did non-lactating females. Their study showed that lactating females tended to reduce their movements during early summer when kits were relatively immobile. They suggested that on the basis of energetic and foraging limitations, lactating females may be more sensitive to changes in habitat quality than other population cohorts. This study is also inconsistent with the hypotheses that the benefits of maintaining exclusive territories is reduced at low mustelid densities (Powell 1993, 1994). Katnik et al. (1994) found that after the removal of resident territorial marten, the remaining martens exhibited intrasexual territoriality with a 5.9% male-male overlap and 10.7% female-female overlap.

In contrast to stoats (Erlinge 1977a, Erlinge & Sandell 1986), male marten did not make forays, or increase or shift the location of their ranges during the breeding season (Katnik et al. 1994). These authors concluded that the energetic cost or predation risk associated with forays outside territories precluded males from wandering during the breeding season in search of potential mates. Males' range size was not correlated with their body mass relative
to females. Further, the area of male ranges did not vary according to the number of overlapping females. Katnik et al. (1994) concluded that energetic requirements related to food availability may have been the major determinant of territory size in the male martens in their study site.

_Fishers:_ Arthur et al. (1989), in their study of adult fishers (*Martes pennanti* L.) in south-central Maine, found that home ranges of females were stable across seasons and years. In contrast males moved extensively from February through April, their ranges shifted between years, and their home ranges overlapped with the ranges of other males during spring. Contrary to Katnik et al. (1994), they found that fishers of both sexes shifted or enlarged their ranges to include areas left vacant when others of the same sex are removed. The seasonal differences between range characteristics of males and females were consistent with Erlinge & Sandell (1986), as range overlap between males increased during spring. Arthur et al. (1989) concluded that maintaining an exclusive breeding territory would not provide a male fisher with exclusive breeding rights, because female fisher ranges overlapped those of several males, rather than being contained entirely within one male's range. Thus, territoriality among fishers probably does not reduce competition for mates. Instead, territoriality may reduce competition for food, because only two adults will usually inhabit a particular area. Therefore, it seems that it is only in those species where female territories usually do not overlap those of several males (e.g., the European otter *Lutra lutra* L.) that the males' territories become more exclusive during the breeding season (Erlinge 1968).
2.2.2 Weasels

*Least weasel*: male least weasels (*Mustela nivalis*) in Stirlingshire, Scotland, exhibit nearly non-overlapping home ranges during winter. During summer the overlap increases although some areas of exclusive use are maintained (Lockie 1966).

In areas of home range overlap, King (1975) pointed out that juvenile female weasels tend to settle close to their birthplace, whereas juvenile males appear to be forced into peripheral areas not occupied by adult males. King, in her study site in an English woodland, never found two resident male weasels occupying the same patch of habitat at the same time. Within the male home range, female least weasels occupy small home ranges that are seldom contiguous and are used exclusively by the resident females (Lockie 1966).

The distribution of weasels in the field has been related to the abundance of small rodents, indicating that food is their main factor in habitat selection (Erlinge 1974). However, changes in the distribution of male weasels recorded by Erlinge (1974) may have been due in part to sexual activity (Lockie 1966, Erlinge & Sandell 1986). Lockie (1966) found that in a dense weasel population, preying on a high density of field voles, male weasels maintained their territories and confined their activity to restricted areas throughout the year. In a deciduous forest in Poland, the home ranges of male weasels radio-tracked during a rodent outbreak were 11-37 ha (minimum convex polygon), compared with 117-216 ha during a low rodent year. The largest recorded weasel home ranges (e.g., 225 ha) have been associated with extremely low densities of rodents (e.g., Jedrzejewski et al. 1995). There may be an energetic limit to expansion of a weasel’s home range, which represents a threshold of territorial behaviour or even the trigger for the extinction of a local weasel population (Jedrzejewski et al. 1995). Moors (1974 cited by King 1989) recorded range areas of 9-16 ha per male in winter, and about 10-25 ha in summer. The few females caught by him had smaller ranges,
averaging 7 ha. Pound (1981 cited by King 1989) using radiotelemetry determined that the winter home ranges of seven males averaged 34 ha, and those of two females, 38 and 12 ha. King (1989) concluded that the difference in area estimates for summer and winter is due to a regular seasonal reorganisation of home ranges, that females occupy smaller areas, that weasels are capable of travelling surprising distances in a short time, and that they avoid each other if they can.

**Stoats:** stoats (*Mustela erminea*) maintain separate home ranges for most of the year. The winter ranges of adult males are large and may include those of several females (Erlinge 1977a, 1979, Powell 1979, King 1982, 1989, King & McMillan 1982). In Ontario, male ranges are 20-25 ha and those of females 10-15 ha (Simms 1979). Stoats usually maintain intrasexual territoriality (Erlinge 1977a, Pounds 1981, Debrot & Mermod 1983, Murphy & Dowding 1994). Furthermore during the non-mating period a male can seldom enter a female territory (intersexual territoriality), even though the female’s territory may lie completely within his own territory. When a male does enter a female’s territory, the two use different parts of that territory (Erlinge 1974, 1977a). Home range and activity of stoats may also be affected by food availability (Erlinge 1977b) and mating behaviour (Erlinge 1977a, Debrot et al. 1985, Erlinge & Sandell 1986). However, when rodents are scarce adult stoats travel widely and do not maintain well-defined home ranges (Debrat & Mermod 1983); the same is true for males when searching for receptive females in spring (Erlinge 1977a, Erlinge & Sandell 1986).

Adult male stoats are dominant to resident members of all sex and age classes except for some pregnant or oestrus females. They have activity schedules and systems of social hierarchy and communication (e.g., mutual avoidance, marking behaviours) (Erlinge 1974, 1977b). The number of young stoats born is closely related to food supplies in spring; this is
well demonstrated by the rapid increase in stoat numbers in New Zealand beech (*Nothofagus*) forest after a heavy seedfall and subsequent rodent irruption (King 1983). After two years of significant seedfall in one such forest, Murphy & Dowding (1994) recorded average home ranges of 206±73 (SE) ha for four male and 124±21 ha for five female stoats, approximately twice the size of ranges in years of low rodent abundance (males 93±7 ha; females 69±8) (Murphy & Dowding 1995). Average home range in spring/autumn of six male stoats was 133±21 ha and of two female stoats was 83±51 ha in coastal grassland, Otago Peninsula, South Island, New Zealand (Moller & Alterio in review). Average overlap in range area among 10 males in this study was 54±11 ha. Alterio (in review) suggested that the small stoat home ranges found in these and other grassland habitats were probably because of a concentration of female stoats and/or prey within habitat patches.

Extensive overlap of intrasexual ranges in stoats has been recorded in spring (Erlinge 1977a, Debrot & Mermod 1983, Erlinge & Sandell 1986). In Sweden, male stoats ranged widely in search of receptive females in spring (Erlinge 1977a, Erlinge & Sandell 1986). Murphy & Dowding (1994) reported that stoats appeared to have exclusive ranges in *Nothofagus* forest in summer, two years after a mast year. However, it remains uncertain whether or not stoats are usually territorial in *Nothofagus* forest (Alterio in review).

### 2.2.3 Ferrets and polecats

**Ferrets:** The ranges of male and female ferrets (*Mustela furo*) overlap extensively but ferrets of the same sex are excluded from at least the centre of each ferret's home range (Moors & Lavers 1981). At Pupepuke Lagoon, North Island (New Zealand), home range of male ferrets averaged 31.3±18.6 ha and that of females 12.4±9.6 ha (Moors & Lavers 1981). In dry tussock grassland habitat, home ranges varied in size from 111 ha for females to 288 ha
for males (Pierce 1987). Moors & Lavers' (1981) female ranges overlapped considerably when prey (*Mus musculus*) availability was high, however Ragg (in review a) noted that Moors & Lavers' (1981) estimates were based on trap locations, with few captures for some individuals, so it was not clear whether the home ranges in their study had been fully revealed. Consequently there may have been more home range overlap than was apparent from the data presented. Ragg (in review a) in Otago, New Zealand, recorded an average home range size of 85.6±9.6 ha for seven males, which was significantly larger than the average of 44.6±8.3 ha for 10 females. She also found an average percentage overlap of 9.2% between male-male pairs, 5.2% for female-female pairs, and 13% for male-female pairs. From these results she concluded that the amount of overlap observed did not support the intrasexual territoriality model, at least for her high density ferret population. However, in her study she recorded more than 20 fixes (number recognised as the minimum acceptable for statistical analysis; Alldredge & Ratti 1986, Gese *et al.* 1988) in only five adults ferrets and overlap range in only one adult male and eight sub-adult or juveniles ferrets with radio-collars (most of her adult ferrets died or disappeared from her study soon after or before radiotracking started). Furthermore, her study was done between February and July (the ferrets' non-mating period), when most of the sub-adult and juveniles ferrets would have still been within their mother's home range (cf. Moors & Lavers 1981, Lavers & Clapperton 1990).

Ragg (in review b) recorded a 7.4% rate of simultaneous den-sharing between February and July 1996. Simultaneous den sharing occurred between adult females pairs, adult male-female pairs, but not between adult male pairs. Simultaneous den sharing also occurred between adult males and juveniles of both sexes and adult females and juveniles of both sexes.
Norbury et al. (in review) in a tussock grassland habitat in New Zealand's South Island recorded ferret home ranges of $102\pm9.9$ ha for 34 males and $76\pm9.1$ ha for 28 females. The percentage of male home ranges that overlapped with other males ranged from 13-34% across sites. Female-female overlap was 11-23%, and overlap between the sexes was 12-31%. Dynamic interaction analysis showed neither avoidance nor attractiveness within and between sexes. With these results, Norbury et al. (in review) supported Moors & Lavers' (1981) conclusion that home range of females overlaps considerably when the abundance of prey (in this case rabbits, *Oryctolagus cuniculus*) is unusually high, consequently they did not find intrasexual territoriality amongst their ferrets. Nevertheless, further analysis of these data indicate that percentage overlap of MCPs (minimum convex polygons) between sexes (30% on average) was significantly larger ($P=0.03$) than between male ferrets (25%) or between female ferrets (23%).

Norbury et al. (in review) found areas of concentrated activity among ferrets. Also, male ferrets' core areas ($27\pm1.5$ ha) were significantly larger than those of females ($16\pm1.5$ ha) with significantly less overlap between core areas than between home ranges.

Norbury et al. (in press) found no significant changes in the mean home range size of ferrets at one site (Bendigo) in dry tussock grassland habitat in New Zealand's South Island after an artificial 77% reduction in rabbit numbers or, on a second site (Earnscleugh), where rabbit numbers remained high. However, at Gray Hills, ferrets increased their mean home range size from 85 ha to $230$ ha when rabbit numbers were reduced by 99%. Furthermore, the proportion of mobile ferrets (i.e., ferrets making forays greater than 1.8 km from their ranges’ centres and later returning, or those that dispersed for longer periods or permanently) in the population increased from 0.04 to 0.33. They also found that the average of 34 male home ranges ($102$ ha) was significantly larger than that of 28 females ($76$ ha).
Polecats: Lodé (1996) described the home range of three pairs of polecats (*Mustela putorius*) in a wetland in western France. The home range of the males averaged $1.31\pm0.34$ km² and that of females $0.39\pm0.04$ km². These polecats tended to exploit a larger area during autumn and winter than during spring and summer. Range overlap between males and females averaged 30.7%. The overlap was greater in spring (43%) and autumn (29%) than in summer (17%) or winter (25%). This overlap of a female polecat’s range by males has also been noted by Blandford (1987), Weber (1989) and Brzezinski *et al.* (1992). Brezezinski *et al.* (1992) in Poland, recorded the linear extent of resident males’ home range as varying from 1.0 to 3.1 km, and those of females from 0.65 to 1.65 km. The home ranges of females were mutually exclusive, but a female range in some cases lay completely within a male’s home range. Male movement predominated in spring most probably because of receptive females; during the mating period female polecats are sedentary (Brzezinski *et al.* 1992).

Lodé (1996) observed that polecats favoured woody and wet areas in western France, where they were apparently hunting small rodents and anurans, respectively. However, it seemed that females avoided making use of those sectors most frequented by males. Lodé (1996) reported that males and females were rarely (i.e. 24 of 453 observations) located simultaneously in the same place. This intraspecific intolerance was particularly obvious during the March breeding season. In summer there was an increase in sightings of polecats together, apparently because young remained together with their mother until autumn. Lodé (1996) concluded that the increase of tolerance between polecats coincided with the increase in food resources (voles and rabbits) during summer and autumn in western France. Nevertheless, the polecats in his study regularly showed a strategy of spatio-temporal avoidance, even between males and females. The polecat’s individualism thus appears to represent an adaptation to the exploitation of patchily distributed resources. Lodé (1996)
concluded that this spatial segregation leads to a social organisation characterised by very individualistic strategies of environment use.

2.2.4 Mink

In Devon, England, the home ranges of mink (*Mustela vison*) tend to be linear, following streams and rivers, although some excursions up small side streams or away from the water were also recorded (Linn & Birks 1980). Mink tended to concentrate their activity in a more restricted portion of their home range during winter (Gerell 1970). The existence of monopolised zones, some used exclusively by the occupants, and others overlapping with neighbours, indicates a territorial system. However, female mink defended their territory against males even though male ranges could encompass one or more female territories (Lockie 1966, Gerell 1970). The home range of females is smaller than that of males, however females appear to use a greater portion of their range more intensely (Linscombe *et al.* 1982). Adult male mink have a home range twice as large as that of the juvenile males. However, when less frequented areas (<5% use intensity) are excluded, the ranges of adult and juvenile males are very similar (Linscombe *et al.* 1982). Core areas could be distinguished within the range, and tended to be associated with high prey availability (Linn & Birks 1980). The home range typically contained about 10 dens, which may be used temporarily or permanently. Mink can be either nocturnal or active both night and day (Linn & Birks 1980). However, the six mink studied by Gerell (1969) were mainly nocturnal in all seasons. Activity tended to increase with increasing length of night and with decreasing temperature. In general, the activity peak of male mink corresponded to the peak in prey activity (Gerell 1969). Female mink showed very little activity during pregnancy, whereas
during lactation females are mainly diurnal and the activity level is considerably higher (Gerell 1969).

In mink, as in other mustelids, territories are maintained by scent marking (Brinck et al. 1978, Kruuk 1978, Erlinge et al. 1982, Macdonald & Mason 1987, Clapperton et al. 1988, Clapperton 1989, Grant & Hawley 1991). Mink in an Idaho study were not strictly territorial and did not actively defend any portion of their home ranges from same sex conspecifics (Jack Whitman cited by Linscombe et al. 1982). In south Scotland, intrasexual home range overlap has been not recorded for mink, and between-sex overlap in territories has been recorded only occasionally (Dunstone & Birk 1972). Differences found in the intensity of use of parts of the home range are best explained by the distribution of food and hunting places (Gerell 1970, Dunstone & Birk 1972, Linscombe et al. 1982). The largest-scale movements in the Swedish mink population involved dispersal of the juveniles, which began in July (summer). Juveniles increased their movements as they increased in size and age. Most juveniles left the study area; some losses were compensated for the following spring as animals from adjacent areas moved in (Gerell 1970). The most obvious seasonal movement in mink (average 18.1 km) in the Montana River were by males in the mating season (Mitchell 1961). However, the majority of the movements for juvenile and adult males in non-mating season did not exceed 4.8 km (Mitchell 1961).

2.2.5 Variation in mustelid territoriality

It is clear from the above review that home range size, degree of overlap and territoriality vary between mustelid species, between studies, and are affected by food availability and season. For example, the changes in territoriality between mink recorded by Gerell (1970) were complex. It was evident that adult females temporarily held territories against an adult
male. However, when a new adult male took over the area used by the females, the females apparently moved to a subordinate position, which also may have involved a restriction of the females’ home ranges. Juvenile males were not allowed to stay within the home range of the adult male, and overlap between adult males left considerable areas of exclusive use. Gerell (1970) recorded that the intensity of use of the home range by mink was affected by territorial behaviour, including guarding behaviours. These movements varied greatly in intensity depending on the status of the defender of the territory and the population pressure. During mating periods, males increased their movements but it seems that those were transitory explorations. For example, a male that visited Gerell’s study area soon returned to his home range located 6 km away. Erlinge (1974) also recorded changes in male weasels’ home ranges during the mating period. Compared with more restricted territorial areas in autumn and winter, male weasels increased their activity in spring, covering larger areas and making only short stops in specific localities. However, he also recorded that males avoided using the same area at the same time during the mating period.

Debrot & Mermod (1983) concluded that during periods when prey abundance was declining, and during the following phase of scarcity, stoats were progressively restricted to a peat-bog area and their territorial system broke down. However, they recorded a significant increase only in the distance of the movements. They did not describe the variation in home range overlap within and between sexes. Further, Simms (1979) recorded no differences in home range size of stoats during both mating and non-mating periods, and did not describe a breakdown of the intrasexual territoriality. He recorded the percentages of a male’s home range overlapping with other males as 36-61%. Percentage overlap during the non-mating period between females and males varied from 25-100%, and females’ home ranges overlapping with males’ home ranges was 31-57%. He concluded that the differences
between his observations and those of Gerell (1970) and Erlinge (1974) were probably an effect of differences in availability of potential mates, food and rate of agonistic interaction because mutual intolerance was leading to avoidance between stoats (Simms 1979). The effect of avoidance in the territorial behaviour in mustelids is also supported by King (1975) and Erlinge (1977a). Similarly, Arthur et al. (1989) recorded increased home range overlap among male fisher during the mating period, but these movements were brief, which suggests territoriality.

It appears that the intrasexual territoriality hypotheses of Erlinger & Sandell (1986), Sandell (1989) and Powell (1993, 1994) are relevant to most of the species reviewed here (Table I). Mustelids' spatial behaviour is strongly affected by variations in food availability during all seasons, and male spatial behaviour is also affected by the availability of receptive females during the mating period. Where the territory of one male does not overlap those of other males, this male will not significantly increase his movements out of his territory during the mating period, but his territory will become more exclusive. The best examples of these behaviours are provided by minks and otters during the mating period (Lockie 1966, Erlinge 1968, Gerell 1970).

Powell (1993, 1994) hypothesised that a female gains nothing from sharing her territory with a male. Therefore, Powell (1994) predicted that a female's access to males is unlikely to be affected by whether the male territories are adjacent to or overlap with hers. Similarly, a female's energy expenditure to find a mate will be minimal because males come to her. Thus Powell argued that intrasexual territoriality in carnivores is imposed on females by males, which are larger than and dominant to females.

Other studies can be interpreted as suggesting that females are affected (either positively or negatively) by intrasexual territoriality, as females under intrasexual territorial situation keep exclusive territories with other females, and the intrasexual territoriality between sexes varies
<table>
<thead>
<tr>
<th>Species</th>
<th>Study location</th>
<th>Range size</th>
<th>Range overlap (%)</th>
<th>Intrasexual territory</th>
<th>Seasonal changes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Within sexes</td>
<td>Attract</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Between sexes</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mustela nivalis</em></td>
<td>England</td>
<td>7-15 ha</td>
<td>1-4 ha</td>
<td>5-75*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela nivalis</em></td>
<td>Poland</td>
<td>11-37 ha</td>
<td>---</td>
<td>UD</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td>Sweden</td>
<td>8-13 ha</td>
<td>2-3 ha</td>
<td>Partly NO</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td>Poland</td>
<td>11.8-109.2 ha</td>
<td>---</td>
<td>NO</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td>Ontario</td>
<td>23 ha</td>
<td>7-13 ha</td>
<td>Partly 32</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td>Switzerland</td>
<td>16.5-24.5 ha</td>
<td>4-10.5 ha</td>
<td>Partly 35.8-60.7</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td>Switzerland</td>
<td>8.8-39.6 ha</td>
<td>1.6-6.4 ha</td>
<td>5-75*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td></td>
<td>11-26 ha</td>
<td>---</td>
<td>&lt;5*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela erminea</em></td>
<td></td>
<td>105-2644 ha</td>
<td>---</td>
<td>40-100*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela putorius</em></td>
<td>Poland</td>
<td>1.6-3.1 km**</td>
<td>0.65-1.65 km**</td>
<td>Partly 0-25*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela putorius</em></td>
<td>France</td>
<td>2.9 km**</td>
<td>---</td>
<td>NO</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela furo</em></td>
<td>New Zealand</td>
<td>&lt;3-7.2 ha</td>
<td>1.9-34.4 ha</td>
<td>&lt;75*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Mustela vison</em></td>
<td>Sweden</td>
<td>11-26 ha</td>
<td>---</td>
<td>&lt;5*</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Martes americana</em></td>
<td>Montana</td>
<td>0.63-3.11 km²</td>
<td>0.06-0.43 km²</td>
<td>Variable Partly 10.7</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No</td>
</tr>
<tr>
<td><em>Martes americana</em></td>
<td>Maine</td>
<td>5.2 km²</td>
<td>2.8 km²</td>
<td>Partly 5.9</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No</td>
</tr>
<tr>
<td><em>Martes martes</em></td>
<td>Poland</td>
<td>65.9-265.2 ha</td>
<td>58.9-121.6 ha</td>
<td>Partly 10.7</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No</td>
</tr>
<tr>
<td><em>Martes martes</em></td>
<td>Finland</td>
<td>14-69 km²</td>
<td>3-14 km²</td>
<td>Partly 3.9</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No</td>
</tr>
<tr>
<td><em>Martes foina</em></td>
<td>Germany</td>
<td>10-61 ha</td>
<td>16-30 ha</td>
<td>Partly 18.7-349.3 ha</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Martes foina</em></td>
<td>Germany</td>
<td>292 ha</td>
<td>185 ha</td>
<td>Partly 292 ha</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
<tr>
<td><em>Martes pennanti</em></td>
<td>Maine</td>
<td>310 ha</td>
<td>185 ha</td>
<td>Partly 310 ha</td>
<td>Yes</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Yes</td>
</tr>
</tbody>
</table>

(*: Inferred from figures in the text, **: range length, ---: no data, NO: no overlap, IM: Intense movement, UD: Undetermined amount of overlap. Intrasexual territoriality was accepted (Yes) or rejected (No) according to the comments of authors on overlaps within and between sexes.)
2.3 Implications of field data for theory

Most authors accept the concept of home range as a restricted area within which individuals or groups live (Jewell 1966), and territory as an area of exclusive use (Lockie 1966). This definition of territory implies priority access to resources and may imply defence by a combination of site attachment and advertisement (e.g., scent marking), which allows for some degree of overlap with conspecifics (Lockie 1966, Voughan & Schwartz 1980, Maher & Lott 1995). However, no author has stated an opinion on the amount of overlap between individuals of the same sex that can occur before the hypotheses of "intrasexual territoriality" is no longer accepted (e.g., Table 1). For example, Powell's (1979, 1994) reviews of variation in territoriality among Mustela and Martes documented levels of intrasexual territoriality that varied from no overlap within sexes to overlap that was substantial but less than occurred between-sexes. Erlinge & Sandell (1986) considered that a significant increase in male home range size, overlap of less than 50% between three males, and from little to complete overlap between three other males' home ranges, was evidence that there was no 'intrasexual territoriality' among male stoats during the mating period. Further, Erlinge & Sandell (1986) concluded that similar behaviours were recorded in mink by Gerell (1970). However, what Gerell (1970) recorded were i) overlaps between male' mink home ranges that varied from no overlap to total overlap and ii) overlap between females' mink home range not larger than 5% (Table I). Furthermore, some such overlaps may be the result of collecting information from dispersing rather than resident individuals, as it is often very difficult to differentiate between the two (Woollard & Harris 1990).

The only study identified in this literature review that assessed intrasexual territoriality by statistical comparison was Katnik et al. (1994), who concluded that within-sex overlap (5.9-10.7%) and between-sexes overlap (37.1-71.4%) were significantly ($P<0.01$) different.
As discussed previously, home range size and spatial organisation in mustelids and other small carnivores are affected mainly by body size, prey availability, breeding season, and social status. They can also vary between habitats and sites. Similar patterns are observed in other carnivore families, including felids, canids and bears (e.g., Brand et al. 1976, Liberg 1984, Fendley & Buie 1986, Griffith & Fendley 1986, Rogers 1987, Coman et al. 1991, Phillips & Catling 1991, Poole 1994, Mirmovitch 1995, Mace & Waller 1997).

Landscape structure plays an important role in the shape, use intensity and overlap of predators' home ranges (Phillips & Catling 1991, Teixeira 1993). Therefore, discussions about variations of intrasexual territoriality should be made by comparing the variation in territoriality among individuals and pairs of the same species within particular study sites, rather than by making comparisons between species or sites (e.g., Katnik et al. 1994, Herrmann 1994). Special care is also needed to avoid misinterpretations arising from the inclusion of transients or juveniles in datasets intended to describe adult behaviour.

2.4 Implications for management of small carnivores

A common goal of furbearer management is to stabilise their population size (Strickland 1994), as the focus internationally is on conservation and harvest of such species. In New Zealand, however, knowledge of small carnivores' home range size and spatial organisation is very important in developing pest control campaigns for these introduced species. If predators maintain fully exclusive territories, each control bait station would be encountered only by a single male and a single female of the same species. Spacing of control stations is thus determined by home range size, which in turn will be influenced by the extent of intra- and inter-sexual territoriality. An understanding of the use intensity and temporal aspects to
territorial behaviour may also be critical for understanding of the epidemiology of how a disease such as bovine tuberculosis is transmitted by that species.

Current information on ferret spatial behaviour in New Zealand mostly relates to the effect of food availability on movement patterns during a part of the year. There are insufficient data at present to determine the extent to which ferrets in New Zealand exhibit intrasexual territoriality. There are a lack of information about variation in territoriality during the non-mating and mating period, and on the effect of ferret social status on spatial organisation. There are also no data to describe use intensity and temporal overlap in feral ferrets’ home ranges. Given this background, the general aim of the following chapters is to contribute to the knowledge about the social and spatial behaviour of feral ferrets in New Zealand, and to assess the importance of food availability, mating period, social status and ferret density as factors that are likely to affect ferrets’ social and spatial behaviour.
Assessing spatial activity in captive feral ferrets, *Mustela furo* L. (Carnivora: Mustelidae)

G. MEDINA-VOGEL

G. J. HICKLING

Department of Entomology and Animal Ecology, P.O. Box 84, Lincoln University, Canterbury, New Zealand

B. K. CLAPPERTON

49 Margaret Avenue, Havelock North, New Zealand

Abstract  We observed eight male and five female feral ferrets (*Mustela furo*) directly and by video recording in an outdoor enclosure consisting of a 36 m\(^2\) arena and six dens and 13 tunnels. We determined their main range and core area sizes, area and use intensity overlap, use intensity of dens and core areas, and temporal overlap between individuals. We assessed the effect of sex, grouping, density, social status and observation period on these activities. From May 1995 to December 1996, six social groups were tested. The spatial patterns identified were consistent with previous studies of free-ranging feral ferrets in New Zealand. Males and females range size were similar. Main range size increased with increasing density, whereas core area use intensity decreased. Dominant males had more temporal
overlap with females than did subordinate males. There was less den sharing within sexes than between sexes. We conclude that intrasexual territoriality was detected and that the described methodology is an effective means of studying, in captivity, aspects of ferret social organisation and behaviour that are difficult to observe in free-ranging animals.

**Key words** *Mustela furo*; ferret; captivity; behaviour; home range; core area; intrasexual territoriality; denning.

**INTRODUCTION**

The ferret (*Mustela furo*) was first introduced to New Zealand in the early 1880s to control rabbit (*Oryctolagus cuniculus*) populations. By the turn of the century, ferrets were well established and had begun to have an adverse impact on native fauna. The first ferret control campaign began in the 1930s (Lavers & Clapperton 1990). New Zealand now has the largest known population of feral ferrets (Lavers & Clapperton 1990). Ferrets have been implicated in the decline of a number of threatened endemic species (Murphy 1996), and as a possible vector of bovine tuberculosis (Tb; *Mycobacterium bovis*) to domestic livestock (Ragg & Walker 1996). Relatively little is known about ferret ecology, movements and social behaviour in New Zealand, yet this information is critical to understanding the effect of ferrets in limiting rabbit numbers, their role in the epidemiology of Tb, and in designing effective predator control programs (King & Moors 1979; Moller et al. 1996; Ragg in review a). This lack of information is due in part to the difficulties and cost of studies to determine spatial patterns and behaviour of free-ranging animals (Harris et al. 1990).

A home range is the more or less restricted area within which an animal moves when performing its normal activities (Harris et al. 1990). Measuring an animal's home range size,
shape and pattern of utilisation is important for most ecological and behavioural studies, particularly those concerned with population density, foraging behaviour, habitat selection, spacing of individuals and their interactions (Harris et al. 1990). Of six radio-tracking studies with ferrets in New Zealand described by Moller et al. (1996), in all but one the sample size was small, the methods of estimation variable, and the number of fixes insufficient to have fully described some home ranges. Furthermore, several of these studies relied on live-trapping or denning for most fixes, which may severely underestimate the home range (Moller et al. 1996; Ragg in review a).

Many aspects of behaviour and spatial patterns of wild ferrets are poorly known, with most observations of ferret and polecats (*Mustela putorius*) behaviour having been made on captive animals (e.g., Poole 1967; 1972; 1973; Biben 1982; Stockman et al. 1986; Clapperton et al. 1988; Clapperton 1989). In this captive study we developed new observation techniques to study the mechanisms underlying ferret spatial patterns and behavioural ecology. We then used these techniques to describe the patterns of spatial activity in ferrets, with the aim of clarifying the results of previous studies on free-ranging feral ferrets.

**METHODS**

**Outdoor enclosure**

We constructed an outdoor enclosure consisting of a 36 m$^2$ arena and six dens and 13 tunnels (Fig. 1b). The arena was enclosed by a 1 m high wire mesh fence buried 0.25 m into the ground (Fig. 1b). Seven plastic tunnels (0.1 m x 0.75 m) with wooden floors were set into the grass-covered soil inside the enclosure. Patches of long grass were left to increase habitat diversity (Fig. 1a). Six den boxes each with one transparent wall, were connected to the enclosure by tunnels. Each den box had two gates, one to close the tunnel
Fig. 1 Sketch of the (a) the grid for determination of space use, (b) the outdoor enclosure (consisting of arena, tunnels and dens) and (c) an example of a separate cage, tunnel and den used for housing individual ferrets between trials. All measurements are in m.
and the other to remove or introduce the ferrets without the need to enter the enclosure (Fig. 1b). Ferrets not currently in experimental use were kept in separate cages (Fig. 1c).

**General procedures**

We conducted 21 trials between May 1995 and January 1996 (termed Replicate I), and 27 trials from May 1996 to December 1996 (termed Replicate II), using different ferrets in each replicate. Replicate I consisted of five social groups and Replicate II of six social groups. These social groups are defined as a ferret alone (For M or F), two males (MM), two females (FF), one male with two females (FFM), two males with one female (FMM), or three males (MMM). Each social group was placed in the enclosure for a trial two or more times during each replicate, depending on the time available in the non-mating and mating periods (which varied between years). These social groups were fed at three different levels of food availability (termed ‘no food’, ‘maintenance’ and ‘double maintenance’).

After capture from the wild, each ferret was kept in an individual cage for at least seven days to habituate it to the food (wild rabbit meat and commercial cat food) and cage conditions. Each was then kept alone for a three-day acclimatisation period in the outdoor enclosure. After every trial we removed each ferret from the enclosure and returned it to its cage until the next trial. We also removed all scats from the enclosure and dens and washed the dens and their tunnels with water to reduce scats and food leftovers.

Ferrets received a ‘maintenance’ level of food throughout the acclimatisation period and while in individual cages. This consisted of 100 g of commercial cat food and/or rabbit meat per day, which maintained adult ferrets at a stable body weight (G. Medina-Vogel pers. obs.). Maintenance food was provided daily by scattering it randomly within the enclosure, half at
sunrise and half at sunset. Double maintenance food was provided by scattering it randomly five times per day, beginning at sunrise and ending at 2300 h.

All ferrets used (two females and three males in Replicate I; three females and five males in Replicate II) were trapped on agricultural land near Christchurch at the beginning of or during each replicate. Two females and two males were juveniles at the time of capture. Each ferret was individually marked with a coloured collar (black, red or white) and ear tags (right ear, left ear, or none).

During each trial of Replicate I, we observed each ferret directly through the glass window of an adjacent building for two hours in the morning and three hours in the evening for each of two days (i.e. a 10-h observation period) and then continuously by a video camera for a further 24-h observation period, giving a total 34-h observation period over three days. Each trial of Replicate II involved a 24-h video observation period, with only sporadic direct observation. Quantitative observations of space use and distribution among ferrets started 8 hours after ferrets were introduced into the enclosure for each trial.

Size of main range and core area

We termed the space used by each ferret inside the enclosure their 'main range'. The enclosure was subdivided into a grid of 30 cells (i.e., 24 arena cells plus six den-and-tunnel cells), which provided a total area of approximately 45 m² (i.e. 1.5 m² per cell; Fig. 1) (adapted from Samuel et al. 1985; Samuel & Green 1988). Each cell’s ‘utilisation frequency’ was assessed by recording the position of each ferret at 5-min intervals, and dividing the total number of cells used by 288 (12 5-min observation hour⁻¹ x 24 hours = 288) for the 24-h observation period, or 408 (12 5-min observation hour⁻¹ x 34 hours = 408) for the 34-h observation period. The total area used by the ferret at some point in their daily activities in
the enclosure was inevitably the full area of the enclosure, so we defined an index of ranging behaviour, which we termed 'Main range'. Main range size was calculated for each ferret at each level of food availability as being the sum of all cells with a frequency of utilisation greater than 0.002 (1/408), divided by 30 and multiplied by the total area of the enclosure (45 m²). We then defined, and ‘core area’ size as being the sum of all cells with a frequency of utilisation greater than 0.3, divided by 30 and multiplied by the total area of the enclosure (45 m²). The use of the value 0.3 is adapted from Harris et al. (1990) and is justified in the results section below (see Fig. 2). The results are presented in m²:

\[
\text{Main range size (m}^2\text{)} = \sum (\text{cells with frequency } > 0.002) \times \frac{45}{30}
\]

\[
\text{Core area size (m}^2\text{)} = \sum (\text{cells with frequency } > 0.3) \times \frac{45}{30}
\]

Use intensity

‘Use intensity’ is a measure that aims to quantify the degree of use of dens or other described areas (e.g. the core area or overlapped area). For example, use intensity of the core area was assessed by summing of the total number of times that a ferret was recorded at 5-min intervals within each core area cell, divided by the total number of five minutes intervals during which observations were being made. The results are presented as frequencies (F).

Intrasexual territoriality

Intrasexual territoriality was assessed by measuring i) area overlap, ii) use intensity overlap, and iii) temporal overlap. Overlap in main ranges and core areas of different ferrets was determined by the total number of cells that was used by more than one ferret during each food test, divided by 30. Overlap in use intensity was determined by adding the minimum
utilisation frequency of each overlapped cell between two or more ferret during each food test (this is termed a Renkonen index; Krebs 1989). Temporal overlap was defined as the sum of all 5 min observation intervals during which a den or the arena of the enclosure was used by two or three ferrets at the same time, divided by the total number of intervals during each test.

Social group were combined into sub-groups to simulated as it would have been if all ferrets in each replicate were at the same time inside an enclosure.

Social status

Each male and female ferret’s social status was assessed by scoring their offensive, defensive, avoidance and submissive reactions (cf. Poole 1967, Erlinge 1977). Ferrets that were seen reacting offensively, which were frequently aggressive toward others, and which won fights in all groups tested were considered dominant. Those that showed submissive postures such as flank shielding, and those that refused to fight by immediately adopting a defensive threat towards the approaching aggressor, were considered subordinates (cf. Poole 1967).

Statistical analysis

The statistical significance of differences in the proportional use of each grid cell by ferrets between replicates was assessed by chi-square test (Fig. 2).

The complicated nature of the main effects and interactions being tested in this study and the impossibility of testing several hundred independent combinations of animals, meant that most effects were replicated and tested as between and within animals effects. For example, most animals were tested in mating and non-mating periods under three feeding regimes, but no ferrets could be included within all social group types and not all ferrets experienced both types of social status. Additionally, the limited on the number of combinations meant that
many higher order interactions could not be evaluated. The data were analysed using SYSTAT's General Linear Model option for unbalanced designs (MGLH; Kirby 1993), in which all effects and estimable interactions were entered. Individual ferrets, or ferrets’ social groups, were also included in the model as 'blocking' effects. The significance of the association between observation period and main range and core area sizes was tested using two way ANOVA. The significance between categories within each factor (sub-groups and food availability levels) was assessed pairwise using Fisher's Least-Significant-Difference tests (LSD). Significance was set at \( P<0.05 \) throughout, and all proportional data were arcsin-transformed before analysis. Standard errors (SE) rather than standard deviations (SD) are given, as the focus of the analysis was on the significance of the different tested variables between treatments.

RESULTS

Size of main range, core area and den use intensity

The overall pattern of ferret spatial activity did not vary significantly \( (X^2=28.0, 19 \text{ d.f.}, P=0.08) \) between replicates (Fig. 2).

Combining both replicates, average main range size was similar \( (F=3.1; 1,200 \text{ d.f.}, P=0.08) \) between males \( (27.7 \pm 0.5 \text{ SE m}^2) \) and females \( (25.0 \pm 0.7 \text{ m}^2) \) (Fig. 3). Average core area estimates were larger for males \( (1.9 \pm 0.2 \text{ m}^2) \) than for females \( (1.7 \pm 0.2 \text{ m}^2) \) \( (F=17.3; 1,200 \text{ d.f.}, P<0.01) \). Main range size and core area use intensity varied significantly with the number of ferrets in the enclosure (Fig. 4), but only main range was affected \( (F=7.1; 1,200 \text{ d.f.}, P<0.01) \) by social status, as dominant individuals recorded larger exclusive territories than subordinates. Den utilisation was not influenced significantly by sex, density or social status.
Spatial overlap

The calculated average main range overlap between males and other ferrets was 20.5±0.5 m² (i.e., 73% of their average main range size), and between females and other ferrets was 16±0.9 m² (i.e., 65% of the average main range size).

Spatial overlap in main ranges was significantly ($F=10.1; 5,215$ d.f., $P<0.01$) affected by the sub-group composition; the largest overlaps being for the male-male and female-male sub-groups (Fig. 5). The average male-male overlap represented 68% of their main range, and the average female-female overlap represented 59% of their range. The male-female overlap represented 71% of the male range and 79% of the female range.

Sex, grouping, density and social status had no significant effect on overlaps of main range and core area.

Use intensity overlap of main range, core areas and dens

Sub-group composition significantly affected the overlap in use intensity of the main range ($F=7.2, 5,215$ d.f., $P<0.01$), core area ($F=7.1, 5,215$ d.f., $P<0.01$) and dens ($F=6.7; 5,215$ d.f., $P<0.01$). Treatment groups containing only or mostly males had less use intensity overlap of main ranges, core areas and dens than did the female and male (FM) sub-groups (Table 1).

The average of use intensity of the same dens (i.e. den sharing) by different ferrets in the social groups was 34% overall. Between males (MM) it was 20%, between females (FF) 30%, and between female and male pairs (FM) 43%.
Fig. 2: Log-transformed frequency of cell use [$\log \left( \sum_{\text{cells used}} \frac{\text{cells used}}{30} + 1 \right)$] plotted against proportional use of each grid cell (pooled data for six different ferret social grouping). The first low value between higher values (at 3.0; see arrows) was used to define ‘core areas’ (adapted from Harris et al. 1990).
Fig. 3: Mean size of main ranges of eight male and five female ferrets in various combinations in the two replicated experiments. Numbers indicate the number of range estimates; error bars indicate ± SE.
Fig. 4: Effect of number of ferrets on size of individual ferrets' main ranges and use intensity of core areas (replicates I and II combined). Numbers indicate the number of estimates made, $P$-values indicate the significance of the difference, error bars indicate $\pm$ SE.
Fig. 5: Effect of sub-group composition on main range overlap for five females and eight males (replicates I and II combined). Sub-groups of ferrets with different letter superscripts differ significantly from each other (Fisher's LSD; $P<0.05$). Numbers indicate the number of range estimates, error bars indicate ± SE.

Temporal overlap of arena and dens

There was significant difference in the temporal overlap of arena ($F=3.5$, 5,215 d.f., $P<0.01$) and dens ($F=7.8$, 5,215 d.f., $P<0.01$) between sub-groups. Sub-groups containing only males (MM) and females (FF) had less den temporal overlap than did female-male pairs (FM) (Table 2). Dominant males had a significantly ($F=5.4$, 1,79 d.f., $P<0.03$) higher arena temporal overlap with females than did subordinates. The average of simultaneous use of the same dens (i.e. temporal overlap) by different ferrets was 7%, between males (MM) 1%, between females (FF) 1% and between female and male pairs (FM) 18%.
Effect of observation period

There was a significant effect of observation period on main range size (Fig. 6; $F=37.8, 2,267$ d.f., $P<0.01$). Estimates based on the 34-h observation period were larger (Fisher's LSD: $P<0.01$) than estimates based on the 24-h and 10 h observation periods (these did not differ significantly) (Fig. 6). However, observation period length had no significant effect on core area size estimates.

![Graph showing the influence of observation period length on the estimated size of the ferrets' main range.](Image)

**Fig. 6:** Influence of observation period length on the estimated size of the ferrets’ main range. Numbers indicate the number of range estimates made, error bars ± SE.
Table 1: Effect of ferret sub-group composition on use intensity overlap (Frequency) of main ranges, core areas and dens. Sub-groups with * differ significantly (Fisher's LSD; P<0.05) from the between-sex overlap (FM). (N) indicate number of overlaps estimates made, (F) indicates frequency, (SE) indicates standard error.

<table>
<thead>
<tr>
<th>Sub-groups</th>
<th>N</th>
<th>Main range (F)</th>
<th>Core area (F)</th>
<th>Dens (F)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(SE)</td>
<td>(SE)</td>
<td>(SE)</td>
</tr>
<tr>
<td>FF</td>
<td>21</td>
<td>0.42</td>
<td>0.30</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.07</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td>FFM</td>
<td>12</td>
<td>0.31</td>
<td>0.22</td>
<td>0.30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.09 *</td>
<td>0.08 *</td>
<td>0.08</td>
</tr>
<tr>
<td>FM</td>
<td>114</td>
<td>0.51</td>
<td>0.42</td>
<td>0.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.03</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>MMF</td>
<td>45</td>
<td>0.21</td>
<td>0.15</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.05 *</td>
<td>0.04 *</td>
<td>0.04</td>
</tr>
<tr>
<td>MM</td>
<td>78</td>
<td>0.28</td>
<td>0.21</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.04 *</td>
<td>0.03 *</td>
<td>0.03</td>
</tr>
<tr>
<td>MMM</td>
<td>6</td>
<td>0.22</td>
<td>0.17</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td></td>
<td>0.13 *</td>
<td>0.12 *</td>
<td>0.12</td>
</tr>
</tbody>
</table>
Table 2: Effect of ferret sub-group composition on temporal overlap in the arena and dens.

Sub-groups with * differ significantly (Fisher's LSD; \( P<0.05 \)) from the overlap between females and males (FM). (N) indicate number of overlaps, (F) indicates frequency, (SE) indicates standard error.

<table>
<thead>
<tr>
<th>Sub-group</th>
<th>N</th>
<th>Arena overlap</th>
<th>Den overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(F) (SE)</td>
<td>(F) (SE)</td>
</tr>
<tr>
<td>FF</td>
<td>21</td>
<td>0.02 0.01</td>
<td>0.02 0.04 *</td>
</tr>
<tr>
<td>FFM</td>
<td>12</td>
<td>0.02 0.01</td>
<td>0.18 0.06</td>
</tr>
<tr>
<td>FM</td>
<td>114</td>
<td>0.03 0.00</td>
<td>0.19 0.02</td>
</tr>
<tr>
<td>MMF</td>
<td>45</td>
<td>0.01 0.01</td>
<td>0.07 0.03</td>
</tr>
<tr>
<td>MM</td>
<td>78</td>
<td>0.01 0.00</td>
<td>0.03 0.02 *</td>
</tr>
<tr>
<td>MMM</td>
<td>6</td>
<td>0.01 0.01</td>
<td>0.05 0.08</td>
</tr>
</tbody>
</table>
DISCUSSION

Spatial activity

The home range of these ferrets was artificially limited by the size of the enclosure, as was animal density (1-3 ferrets/45 m$^2$). The results of the study were nevertheless broadly consistent with those described by Ragg (in review a) and Norbury et al. (in press) for free-ranging feral ferrets in New Zealand. For example, males had similar main ranges than did females, and the ranges of neighbouring males (MM) overlapped more than did the ranges of neighbouring females (FF). The extensive main range overlap between ferrets found in this study was, however, probably an effect of the enclosure conditions as, for example, river otters (Lutra canadensis) confined to narrow stream corridors showed unusually extensive home range overlaps (Hornocker et al. 1983).

Previous descriptions of feral ferrets' spatial activity in New Zealand are contradictory. Moors and Lavers (1981) concluded from their study in the North Island that ferrets exhibit intrasexual territoriality, as home ranges of males and females overlapped extensively whereas most ranges of individuals of the same sex overlapped only near the borders. However, Ragg (in review a) and Norbury et al. (in review) both suggested that intrasexual territoriality was not obvious in study sites which had abundant rabbit prey and high ferret population densities. Sandell (1989) predicted that overlapping ranges containing enough food for several individuals should be larger than exclusive ranges including food for one individual. Contrary to Ragg's (in review b) suggestions that one of the reasons that intrasexual territoriality was absent between ferrets in her study site may have been their high population density, our results suggest that density per se does not seem to affect intrasexual territoriality. Other field studies on carnivores have reached similar conclusions. For example,
Katnik et al. (1994) found that after the removal of territorial resident marten (*Martes americana*), remaining martens continued exhibiting intrasexual territoriality.

Furthermore, our results suggest that intrasexual territoriality cannot be described simply in terms of spatial overlap; it also involves use intensity and temporal overlap. Again, similar observations have been made on other carnivores including wild polecats (Lodé 1996) and grizzly bears (*Ursus arctos horribilis*) (Mace & Waller 1997). In North American wolverines (*Gulo gulo*), scent marking serves to maintain spacing in time rather than in area (Hornocker et al. 1983). Similarly Clapperton et al. (1988) described an olfactory communication system in ferrets by which such a spatio-temporal social organisation system could be mediated.

Although the ferrets in our enclosure had high overall range overlap, we found that the mechanisms leading to intrasexual territoriality nevertheless remained apparent. This was evident from the less-than-complete spatial overlap of their main ranges, the reduced use intensity overlap of main range and core area in the areas and dens, and the limited temporal overlap of arena and dens by members of the same sex, particularly males. We also found that intrasexual territoriality was significantly affected by the sex and group structure of the ferrets, but not by density *per se*.

These observations are supported by studies in an intensively harvested population of marten (*Martes americana*) in Maine (USA), which maintained the same spacing pattern (intrasexual territoriality) as described for unharvested populations (Katnik et al., 1994) and for wild polecats (Lodé 1996).

Ragg (in review b) recorded a 44.3% rate of sequential den-sharing and a 7.4% rate of simultaneous den-sharing between feral ferrets, and Norbury et al. (in review) recorded 4.9% simultaneous den-sharing in a nearby population. In this captive study we found similar and simultaneous den sharing percentages (25% and 7%, respectively). We also showed that den
sharing is consistent with the intrasexual territoriality distribution and is affected by sex, and group composition.

**A critique of this captive-animal methodology**

The total space use by the ferrets in the enclosure was obviously the area limited by the enclosure. So what the ‘main range’ and ‘core area’ provided was not measure of variation in the extent of space use but rather an index of territorial behaviour. Ferrets are highly mobile animals with home ranges size between 12 ha to 288 ha (Moors & Lavers 1981, Pierce 1987, Ragg in review a, Norbury *et al.* in review) and so when they were placed in the enclosure they typically explored all 30 cells of the arena with the first hour or so (Medina-Vogel pers. obs.), over the next 8 h the spatial relationship of the ferrets stabilised rapidly, so we were confident that the difference we subsequently studied were due to territorial rather than exploratory behaviour. This was evident from the differences in spatio-temporal overlaps and exclusiveness according to variations in sub-group, social status and density (all of which tend to support the intrasexual territorial model for small carnivores). Therefore, a decrease in main range size, together with less area overlap between two ferrets were interpreted as a tendency toward exclusiveness rather than a decrease in range size.

As with free ranging mammals (where home range size estimates increase as more location points are obtained; Harris *et al.* 1990), an increase in observation period in this study led to an increase in the estimated main range size (Fig. 6). To avoid an excessive effect of the enclosure on the amount of overlap measured between individuals, it was therefore important to record the individuals’ spatial patterns before the main range size estimates plateau at 100% of the enclosure size. In this study this plateau was being approached probably after 34 h of observation (Fig. 6).
Temporal overlap analysis could have been done by estimating the individual overlap as a percentage of the individual total denning time. However, in all the trials the ferrets spent more than 80% of their time resting inside the dens, so we instead chose to calculate overlap as a proportion of total observation time.

The method we used in this study to determine main ranges and core area size (as a measure of territoriality) showed realistic variations amongst males and females, animal groupings and social status. An alternative procedure for determining core area presented by Samuel et al. (1985) and Samuel & Green (1988) used the grid cells containing a significantly greater proportion of records than the mean. Applying that method to the present study would have resulted in the core area being a much larger proportion of the overall main range area than is normally seen in field studies (cf. Harris et al. 1990). Instead, determining the core area at the first low value between two higher frequency values (see Fig. 2); adapted from Harris et al. 1990) provided a realistic relationship between size of main range and core area that changed in a meaningful way according to the animals’ responses (Medina-Vogel pers. obs.).

By analysing main range size and use intensity patterns using continuous observations we avoided the potential biases inherent in behaviour sampling (for example the incomplete assessment of overlap in use intensity that results from short sampling periods; cf. Beyer & Haufler 1994).

We conclude that the methodology trialed here is appropriate for determining some aspects of ferret territoriality, behaviour and spatial patterns in captivity. In subsequent papers we use this methodology to determine how food availability and breeding conditions influence captive ferret territoriality and behaviour.
ACKNOWLEDGMENTS

We are grateful to the Department of Entomology and Animal Ecology, Lincoln University, for providing research facilities and funding. We also are grateful to the New Zealand Ministry of Foreign Affairs and Trade for the NZODA Postgraduate Full Scholarship that supported Gonzalo Medina-Vogel’s studies. Dr. Chris Frampton provided excellent statistical advice.

REFERENCES


Harris, S.; Cresswell, W. J.; Forde, P. G.; Trewhella, E. J.; Woollard, T.; Wray, S. 1990: Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal review 20: 97-123.


Kirby, K. N. 1993: *Advanced data analysis with SYSTAT.* New York, Van Nostrand Reinhold.


CHAPTER FOUR

Spatial activity of captive feral ferrets (*Mustela furo* L.): the effect of food availability and the mating period.

GONZALO MEDINA-VOGEL*, GRAHAM J. HICKLING* & B. KAY CLAPPERTON**

*Department of Entomology and Animal Ecology, P.O. Box 84 Lincoln University, Canterbury, New Zealand.

**49 Margaret Avenue, Havelock North, New Zealand.

Paper prepared for Animal Behaviour

Abstract. We observed eight male and five female captive feral ferrets (*Mustela furo*) directly and by video recording in an outdoor enclosure consisting of a 36 m² arena and six dens and 13 tunnels. We assessed the effect that three levels of food availability, and the mating season had on main range and core area sizes, use intensity of the arena, dens and core areas, and spatial and temporal overlap between individuals. The experiment involved two replicate trials, involving five and six social groups respectively. Ferrets' main range varied with changes in food availability, with a decrease in main range size at no food availability
being more evident in males than in females. Changes in food availability had no effect on the level of intrasexual territoriality among the captive ferrets. During the non-mating period, the presence of subordinate males induced a change in social dominance in favour of the adult females. During the mating period, both male and female ferrets increased their main range size and reduced their time spent denning. During the mating period dominant males increased their overlap with females and their exclusion of subordinate males. As females were a more predictable resource than food availability in this study, the removal of the female during the mating period induced a decrease in the exclusiveness of territoriality between males. The results are discussed in relation to Powell’s (1993, 1994) intrasexual territoriality model, and Erlinge & Sandell (1986) and Sandell’s (1989) predictions of variation in small carnivore range and territoriality. We propose a refined model for variation in home range, territoriality and dispersal of solitary, sexual dimorphic carnivores in relation to changes in prey abundance, mating period and social status. The implications of these captive observations for control of pest populations of ferrets in New Zealand are discussed.

*Effect of the mating period on spatial activity of* Mustela furo

Members of the genera *Mustela* and *Martes* are mainly solitary except for reproductive purposes; males and females share the same area, but will exclude others of the same sex. This system is termed ‘intrasexual territoriality’ (Powell, 1979). Territoriality and non-territoriality are alternative patterns of social organisation that are chosen by individual carnivores in their attempts to survive and maximise reproductive success (Sandell 1989). An individual may be expected to change from a territorial to a non-territorial type of behaviour when a threshold is reached beyond which the cost of territoriality exceeds its benefits (Krebs
This means that the spacing pattern in a population is the result of the tactics chosen by the individuals in their attempts to survive and maximise reproductive success (Sandell 1989). Resource availability may therefore affect mustelid social organisation (Erlinge & Sandell 1986, Powell 1994). Powell (1993, 1994) predicted that as prey populations vary from very low to very high densities, populations of solitary, sexually dimorphic carnivores will change their use of space in the following sequence:

transient → individual territories → intrasexual territories → extensive home range overlap

It is thought, therefore, that some solitary carnivores exhibit intrasexual territoriality because the spatial and temporal distribution of the most likely limiting resource for these species (food) allows for a trade-off between food and reproductive requirements not available to species with individual territories. This in turn allows male spacing to be affected by female spacing, as well as by the distribution of food (Powell 1993). Erlinge & Sandell (1986) and Sandell (1989) argued, that female spacing patterns are primarily determined by the abundance and distribution of food, whereas male spatial organisation, at least during the mating season, is determined by the distribution of females. If one resource is the critical factor for males in one season (e.g., food in winter) and the other critical during another season (e.g., mates in spring), and if the two resources have different spatial characteristics, then changes in relative importance of the resources can induce changes in the social organisation of the population between the mating and the non-mating season (Erlinge & Sandell 1986, Sandell 1989). Furthermore, male ranges should tend to be relatively exclusive when females are abundant and evenly distributed, whereas they should tend to overlap when females are the limiting resource (Sandell 1989).
Ferrets (*Mustela furo*) were first introduced to New Zealand in the early 1880s to control rabbits (*Oryctolagus cuniculus*) and quickly established feral populations. Ferrets have a promiscuous mating system and exhibit territorial behaviour (Moors & Lavers 1981, see Chapter 3). However, both Ragg (in review) and Norbury et al. (in review) have suggested that ferrets in New Zealand have higher rates of social contact than do other solitary mustelid species, and that the different conclusions of the various studies undertaken to date may be attributed to differences in ferret density and spatial behaviour relative to prey density at the various study sites. In this chapter we investigated changes of spatial activity of captive feral ferrets at different levels of food availability and compared our results with the predictions of current models of carnivore home range and territoriality. Specifically, we use data on feral ferrets’ spatial behaviour in captivity to test the hypotheses that during the mating season i) there is a change in the social organisation of the males, resulting from the shift between food and females as the seasonal decisive resources, and ii) there is no equivalent change for females.

**METHODS**

**Outdoor enclosure**

We constructed an outdoor enclosure consisting of a 36 m² arena and six dens and 13 tunnels. The arena was enclosed by a 1 m high wire mesh fence buried 0.25 m into the ground (see Chapter 3). Seven plastic tunnels (0.1 m x 0.75 m) with wooden floors were set into the grass-covered soil inside the enclosure. Ferrets not currently in experimental use were kept in separate cages (see Chapter 3).
General procedures

We conducted seven trials during the non-mating period (May to July 1995) and 14 trials during the mating period (July 1995 to January 1996) (termed Replicate I). A further 15 trials were conducted during the non-mating period (May to September 1996) and 12 trials during the mating period (September to December 1996) (termed Replicate II). Different ferrets were used in each replicate. The start of the mating period was indicated by increased abdominal scent marking and body contact between males and females, and confirmed by subsequent observation of copulation (cf. Poole 1967, Clapperton 1989, Grant & Hawley 1991). Replicate I consisted of five social groups and Replicate II of six social groups; a ‘social group’ was defined as a group of ferrets (i.e., a ferret alone, two males, two females, one male with two females, two males with one female, or three males) placed in the enclosure for a trial. Ferrets in each social group were tested with three levels of food availability (termed ‘no food’, ‘maintenance’ and ‘double maintenance’). After capture from the wild each ferret was kept in a separate cage for at least seven days to habituate it to the food (rabbit meat and commercial cat food) and cage conditions. Each was then kept alone for a three-day acclimatisation period in the outdoor enclosure. After every trial we removed each ferret from the enclosure and returned it to its cage until the next trial. We also removed all scats from the enclosure and washed the dens and tunnels with water to remove remaining scats and food leftovers.

During Replicate I, we observed each ferret directly through the glass window of an adjacent building for 2-h in the morning and 3-h in the evening for each of two days, and continuously for 24-h using a video camera, for each level of food availability. During each trial of Replicate II, we relied the video camera for 24-h, with sporadic direct observation, for each level of food availability.

Ferrets received a ‘maintenance’ level of food throughout the acclimatisation period and
while in individual cages. This consisted of 100 g of commercial cat food and/or rabbit meat per day, which maintained an adult ferret without loss or gain in body weight (G. Medina pers. obs.). Maintenance food and double maintenance food were provided daily by scattering it randomly in the enclosure.

All ferrets in the study (two females and three males in Replicate I; three females and five males in Replicate II) were trapped near Christchurch at the beginning or during each replicate. Two females (Replicate I) and two males (Replicate II) were juveniles at the time of capture. Each ferret was individually marked with a coloured collar (black, red or white) and ear tag (right ear, left ear, or none).

**Space use intensity**

The enclosure was subdivided into a grid of 30 cell (24 arena cells plus six den and tunnel cells) providing a total area of approximately 45 m² (i.e. 1.5 m² per cell) (see Fig. 1, Chapter 3). Each cell’s utilisation was assessed by recording the position of each ferret at 5-min intervals, and subdividing the total number of cells used by 288 and 408 times for the 24-h and 34-h observation periods, respectively. Main range size was defined for each individual ferret, at each level of food availability, as being the sum of all cells with a frequency of utilisation greater than 0.002, divided by 30. Core area size was defined as being the sum of all cells with a frequency of utilisation greater than 0.3, divided by 30 (see Chapter 3 for more detail).

Use intensity of the core areas was defined as the sum of the total number of times that a ferret was recorded at 5-min intervals on each core area cell, divided by the total number of 5-min intervals for which it was observed during each trial. These data were presented as frequencies (F) (see Chapter 3).
**Intrasexual territoriality**

Intrasexual territoriality was assessed by measuring i) area overlap, ii) use intensity overlap, and iii) temporal overlap (see Chapter 3). Overlap in main ranges and core areas of different ferrets was determined by the total number of cells used by more than one ferret during each test divided by 30. Overlap in use intensity was determined by adding the minimum utilisation frequency of each overlapped cell between two or more ferret during each food test (termed a Renkonen index; Krebs 1989). Temporal overlap was defined as the sum of all 5 min observation intervals during which a den or the arena were used by two or three ferrets at the same time, divided by the total number of intervals during each test (see Chapter 3).

Social groups were combined into six different sub-groups: two females (FF), one females and one males (FM), two females and one males (FFM), one females and two males (FMM), two males (MM) and three males (MMM).

Each male and female ferret’s social status was assessed by scoring their offensive, defensive, avoidance and submissive reactions (cf. Poole 1967, Erlinge 1977). Ferrets that were seen reacting offensively, which were frequently aggressive toward others, and which won fights in all groups tested were considered dominant. Those that showed submissive postures such as flank shielding, and those that refused to fight by immediately adopting a defensive threat towards the approaching aggressor, were considered subordinates (cf. Poole 1967).
Statistical analysis

The complicated nature of the main effects and interactions being tested in this study, and the impossibility of testing several hundred independent combinations of animals, meant that most effects were replicated and tested as between-and within-animals effects. For example, most animals were tested in mating and non-mating periods under three feeding regimes, but no ferrets could be included within all social group types and not all ferrets experienced both types of social status. Additionally, the limited number of combinations meant that many higher order interactions could not be evaluated. The data were analysed using SYSTAT's General Linear Model option for unbalanced designs (MGLH; Kirby 1993), in which all effects and estimable interactions were entered. Individual ferrets, or ferrets' social groups, were also included in the model as 'blocking' effects. The significance between categories within each factor (sub-groups and food availability levels) was assessed pairwise using Fisher's Least-Significant-Difference tests (LSD). Significance was set at $P<0.05$ throughout, and all proportional data were arcsin-transformed before analysis. Standard errors (SE) rather than standard deviation (SD) are given, as the focus of the analysis was on the significance of the different tested variables between treatments.
RESULTS

Effect of food availability

Main range size and area overlap

Changes in food availability significantly \((F_{2,200}=4.2, P<0.02)\) affected the overall main range size of estimates for the captive ferrets. However, the observed reduction of the main range size at the no food level relative to the maintenance food levels was significant only for males (Fig. 1; Fisher's LSD: \(P<0.05\)), and was not different from double maintenance food level. There was no effect of food availability on core area size, area use intensity or den use intensity.

Males had 0.3 m\(^2\) larger core areas than did females, and as the number of ferrets in the enclosure increased, the effect of food availability on the differences in core area size between males and females became more pronounced \((F_{2,200}=3.6, P<0.03)\).

Main range overlap in area varied significantly \((F_{5,215}=3.1, P<0.01)\) amongst food availability levels for the study as a whole. The smallest overlap (Fisher's LSD: \(P<0.05\)) was with no food availability. There was no effect of food availability on core area and den overlap.

Intrasexual territoriality and differences between the ferret sub-groups

Main range overlap between females and males \((F_{2,79}=4.5, P<0.02)\), and overlap between all ferrets in the various sub-groups \((F_{5,215}=3.1, P<0.05)\), were both affected significantly by variation in food availability (Table I). While territoriality between females and males \((FM)\) and within male \((MM)\) groups become more exclusive when food was scarce, territoriality within female groups \((FF)\) become more inclusive. In contrast, food availability had no effect
(F_{10,215}=1.0, P=0.44) on intrasexual territoriality (i.e. the overlap within sexes relative to the overlap between sexes).
Table I. Effect of food availability on the area overlap of ferret main ranges for the various different sub-groups. Results with different letters are significantly different (Fisher's LSD: $P<0.05$). DFM: double food maintenance, FM: food maintenance, NF: no food, N: number of overlap estimates, (SE): ± standard error.

<table>
<thead>
<tr>
<th>Social group</th>
<th>Main range overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
</tr>
<tr>
<td>FF</td>
<td>21</td>
</tr>
<tr>
<td>FFM</td>
<td>12</td>
</tr>
<tr>
<td>FM</td>
<td>114</td>
</tr>
<tr>
<td>MMF</td>
<td>45</td>
</tr>
<tr>
<td>MM</td>
<td>78</td>
</tr>
<tr>
<td>MMM</td>
<td>6</td>
</tr>
</tbody>
</table>

The effect of the mating period

Main range size, core area size, use, and dens use intensity

During the mating period, ferrets increased their main range size ($F_{1,200}=11.2$, $P<0.01$) (Fig. 2). Similarly, both male (1.6 m$^2$ to 2.0 m$^2$) and female (1.6 m$^2$ to 1.8 m$^2$) ferrets increased the size of their core area ($F_{1,200}=5.1$, $P<0.03$), and reduced the use intensity of their core areas ($F_{1,200}=6.5$, $P=0.01$) and dens ($F_{1,200}=11.7$, $P<0.01$) (Fig. 3).
These effects resulted primarily from a change in spatial behaviour by the dominant males and females (Fig. 4). During Replicate I there was no dominant female, whereas during the non-mating period in Replicate II many (17 of 45; 38%) dominance interactions were won by females.

**Intrasexual territoriality and differences between the ferret sub-groups**

There was a significant \((F_{1,215}=17.9, P<0.01)\) effect of the mating period on the overlap of main ranges between ferrets in all sub-groups. During the mating period, there were significant increases in male-female spatial overlap in main ranges \((F_{1,79}=12.2, P<0.01)\) (Fig. 5), and temporal overlap in use of the arena \((F_{1,79}=8.1, P<0.01)\) and the dens \((F_{1,79}=4.2, P<0.05)\). There was also a reduction of males’ main range use intensity overlap (for \(MM\)) and main range overlap (for \(MMM\)) (Fig. 5). Dominant males overlapped their main ranges \((F_{1,79}=10.5, P<0.01)\) with females significantly more than did subordinate males. Dominant males spent also significantly \((F_{1,79}=8.1, P<0.01)\) more time together with females in the arena than did subordinate males (Table II).

During the mating period there was a significant difference between sub-groups in the amount of temporal overlap in the arena \((F_{5,215}=2.3, P<0.05)\) and in dens \((F_{5,215}=6.6, P<0.01)\). Temporal overlap in den use between males and females became significantly (Fisher’s LSD; \(P<0.05\)) higher than within male groups or within female groups; furthermore the temporal overlap within these single-sex groups was not affected by the mating period (Table III). The high overlap recorded by the \(FFM\) and \(MMF\) sub-groups was arouse in part because ferrets in those groups were commonly recorded resting at the same time in the same den on frosty mornings. During the mating period, the main range overlap between males was less when a
female was present (13.5 m² \( MMF \)) than when there was no female in the sub-group (16.3 m² \( MM \); \( F_{1,79}=6.2, P<0.02 \)).

**Figure 2.** Mean size of main ranges of eight male and five female ferrets in the non-mating and mating periods in two replicate experiments combined. Numbers indicate the number of range estimates, error bars indicate ± SE.
Figure 3. Den use intensity by eight male and five female ferrets in the non-mating and mating periods in two replicate experiments. Numbers indicate the number of use intensity estimates, error bars indicate ± SE.
Figure 4. Differences between three dominant and five subordinate male ferrets mean size of main ranges in the non-mating and mating periods in two replicate experiments. Numbers indicate number of range estimates, error bars indicate ± SE.
Table II. Effect of social status of eight male ferrets on overlap with five females during non-mating and mating periods.


<table>
<thead>
<tr>
<th>Period</th>
<th>Social status</th>
<th>N</th>
<th>Overlap of area</th>
<th>Temporal overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Main range</td>
<td>Arena</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(m²) (SE)</td>
<td>(F) (SE)</td>
</tr>
<tr>
<td>Replicate I</td>
<td>Non-mating</td>
<td>3</td>
<td>19.1 2.90</td>
<td>0.01 0.01</td>
</tr>
<tr>
<td></td>
<td>Subordinate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dominant</td>
<td>3</td>
<td>14.0 2.90</td>
<td>0.01 0.01</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subordinate</td>
<td>15</td>
<td>23.0 1.40</td>
<td>0.07 0.01</td>
</tr>
<tr>
<td></td>
<td>Dominant</td>
<td>15</td>
<td>25.6 1.40</td>
<td>0.01 0.01</td>
</tr>
<tr>
<td>Replicate II</td>
<td>Non-mating</td>
<td>21</td>
<td>17.0 1.10</td>
<td>0.01 0.01</td>
</tr>
<tr>
<td></td>
<td>Subordinate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dominant</td>
<td>21</td>
<td>13.5 5.10</td>
<td>0.01 0.01</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Subordinate</td>
<td>16</td>
<td>17.6 1.32</td>
<td>0.01 0.01</td>
</tr>
<tr>
<td></td>
<td>Dominant</td>
<td>16</td>
<td>21.1 1.32</td>
<td>0.07 0.01</td>
</tr>
</tbody>
</table>
Table III. Differences in temporal overlap of arena and dens between the non-mating and mating periods for two females (FF), two females and one male (FFM), one female and one male (FM), two males and one female (MMF), two males (MM) and three males (MMM). (N): number of overlap estimates, (F): frequency, (SE): standard error, *: Fisher’s LSD; $P<0.05$.

<table>
<thead>
<tr>
<th>Ferret sub-group</th>
<th>Period</th>
<th>N</th>
<th>Arena (F)</th>
<th>Arena (SE)</th>
<th>Dens (F)</th>
<th>Dens (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>FF</td>
<td>Non-mating</td>
<td>18</td>
<td>0.02</td>
<td>0.01</td>
<td>0.03</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td>3</td>
<td>0.02</td>
<td>0.01</td>
<td>0.16</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>FFM</td>
<td>Non-mating</td>
<td>9</td>
<td>0.02</td>
<td>0.01</td>
<td>0.21</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td>3</td>
<td>0.02</td>
<td>0.01</td>
<td>0.02</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
<td></td>
</tr>
<tr>
<td>FM</td>
<td>Non-mating</td>
<td>48</td>
<td>0.00</td>
<td>0.00</td>
<td>0.02</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td>66</td>
<td>0.03</td>
<td>0.00</td>
<td>*</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>MMF</td>
<td>Non-mating</td>
<td>15</td>
<td>0.02</td>
<td>0.01</td>
<td>0.17</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td>30</td>
<td>0.02</td>
<td>0.01</td>
<td>0.01</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>MM</td>
<td>Non-mating</td>
<td>30</td>
<td>0.02</td>
<td>0.00</td>
<td>0.11</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td>48</td>
<td>0.02</td>
<td>0.00</td>
<td>0.07</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>MMM</td>
<td>Non-mating</td>
<td>3</td>
<td>0.03</td>
<td>0.00</td>
<td>0.06</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Mating</td>
<td>3</td>
<td>0.01</td>
<td>0.00</td>
<td>0.13</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
</tr>
</tbody>
</table>
Figure 5. Mean area overlap between main ranges of eight males and five females in FM groups of ferrets and common area overlap between five males in males MMM groups during the non-mating and mating periods. Bars with different letters within sub-groups are significantly different (Fisher’s LSD: $P<0.05$). Numbers indicate the number of overlap estimates, error bars indicate ± SE.
DISCUSSION

Effect of food on ferrets’ spatial activity

Powell’s (1993) model predicts when prey density is high, extensive overlap of individual predators’ home ranges is expected. Conversely, when prey are scarce, reduced overlap or individual territories are predicted. Our observations on range area overlap are consistent with Powell’s predictions. Ferrets (especially males) showed extensive overlap at double food maintenance, and less overlap at no food availability. Similarly, Moors & Lavers (1981) found that home ranges of female ferrets overlapped extensively at their study site when the abundance of mice (Mus musculus) was unusually high.

Sandell (1989) predicted that when food resources varied overlap between ranges should be expected, and that overlapping ranges would be larger than exclusive ranges. The degree of overlap will then be controlled by boundary defence by way of aggressive interactions and/or scent marking (Lockie 1966, Clapperton et al. 1988, Maher & Lott 1995, see Chapter 3). A true expansion of home range size, or dispersal, is obviously not possible in our experimental enclosure. Nevertheless, our methodology demonstrated that an increase in food availability was associated with a reduction in territoriality, as predicted by both Sandell (1989) and Powell (1993, 1994). Conversely, when food was scarce the captive ferrets recorded tried to maintain more exclusive territories, again as predicted by both Sandell and Powell. In this situation the increase in aggressive interactions which had the potentially to end in fights, instead resulted in increased avoidance behaviour. These small main ranges, and the difference in variation in core areas size between sexes, support the view that exclusive main ranges and core areas were use during the time of food shortage for avoidance rather than foraging, and thus provided a better mechanism to maintain territory (as proposed by Griffith & Fendley 1986, Krebs & Davies 1987). Similarly, Debrot & Mermod (1983)
observed in the field that during the initial phase of prey scarcity, female stoats were progressively restricted to one area.

This pattern of intrasexual territoriality was unaffected by variation in food availability. Therefore, it seems that variation in range area overlap may be primarily a function of the size of the respective main ranges and core areas rather than a function of variation in intrasexual territoriality. Female ferrets may be less likely than males to overlap their ranges with other ferrets (especially other females) because their ranges are small; conversely males are likely to have large proportions of their ranges overlapping with other ferrets' ranges simply because they have large ranges. This is supported by field observations in the South Island of New Zealand: overlap between male-male pairs averaged 9.2% in one area where ranges average 86 ha (Ragg in review), whereas it was 24.7% in another area where males had 102 ha (Norbury et al. in review).

**Effect of the mating period on ferrets' spatial activity**

Increased male mobility during the mating period has been reported in several mustelid species (Lockie 1966, Gerell 1970, King 1975, Erlinge 1974, 1977, Debrot & Marmod 1983, Hornocker et al. 1983, Arthur et al. 1989, Brezezinski 1992) and the same pattern was evident in this captive study. However, our female ferrets increased their main ranges during the mating period, contrary to what has been described for polecats (*Mustela putorius*) in Poland (Brezezinski et al. 1992), and wolverines (*Gulo gulo*) in North America (Hornocker et al. 1983). However, territorial behaviour (expressed as reduced overlap with other females compared with overlap with males) was maintained or become stronger during the mating season. Similar behaviour has been described in wild stoats (*Mustela erminea*) (Erlinge 1983). The small main ranges and minimal roaming behaviour shown by our ferrets during
the non-mating period (mostly autumn and winter) and by other carnivores in the wild (Powell 1994) may have evolutionary significance. Ferrets are less active and less territorial during cold months, perhaps because the energy cost of territorial defence is too high to maintain this behaviour year round.

Ragg (in review) reported that 7.4% of her radiotelemetry fixes involved simultaneous den-sharing between feral ferrets during the non-mating period (February-July) in Otago, New Zealand. Similarly, we found that during the non-mating period an average of 7% of a typical ferret's time budget involved simultaneous den-sharing. However, we also found that during the mating period simultaneous den-sharing between females and dominant males increased to an average of 47%, and between females and subordinate males to an average of 9%.

As has been described for male European river otters (*Lutra lutra*) (Erlinge 1968, Kruuk & Moorhouse 1991, Durbin 1996), our dominant and subordinate captive feral male ferrets altered their spatial activity during the mating period in different ways, which suggests that they have different mating tactics (cf. Sandell 1986, 1989). Dominant male ferrets' spatial activity was highly correlated with the females' spatial activity. Dominant males increased their main range area and overlap in use intensity with females during the mating period, whereas subordinate males were more sedentary, moving occasionally between dens and core areas. For a dominant male in the wild, a roaming tactic is likely to be profitable during the mating period, since his social status allows him access to several females. In contrast, our captive male ferrets maintained exclusive territories during the mating period. This is contrary to observations on several other male mustelids (Erlinge 1974, 1977, Debrot & Marmod 1983, Arthur et al. 1989), although this behaviour has been described in European river otter (Erlinge 1968). As our ferrets' range area was artificially limited by the enclosure, maintenance of a territory may have benefited our dominant males by providing them with
exclusive mating opportunities with females living entirely within their territories (cf. Sandell 1989). Social dominance in favour of our captive female ferrets during the non-mating period (Replicate II) has also been observed in free-ranging European polecats (Lodé 1996). However, these behaviours could not be attributed in our case to protection of the litter after parturition (cf. Lodé 1996). It is more probable that the observed change in social dominance was attributable to the presence of two juvenile males, since during the non-mating period in Replicate II, only one of the three males was adult.

Erlinge & Sandell (1986) predicted that, for mustelids with typical intrasexual territoriality, the males’ territorial system would vary as they alternated between food and females as two different ‘critical’ resources during the non-breeding and breeding seasons. As females in this study could not leave the enclosure, and there was only one dominant male with access to them, females in oestrus were not a variable resource. Therefore, the decrease intrasexual territoriality (i.e., increased overlap) between our captive male ferrets when females were removed from the enclosure during the mating period seems likely to have represented a change in behaviour induced by the variability of the new critical resource (food), since exclusive territories to maximise access to matings was no longer necessary.

Variation in captive feral ferrets’ intrasexual territoriality

Our observations on the effect of food and mating period on captive ferret’s spatial behaviour support Powell’s (1993, 1994) model. However, we believe that the model can be refined by incorporating additional factors so that it encompasses social status, sex, density and the mating period (Fig. 6).

Fig. 6 suggest that there is a resource threshold that needs to be reached before intrasexual territoriality breaks down. In this study this is particularly supported by the variation in
overlap of main ranges between males ferrets recorded at the no food level. While males in
sub-group of two males (MM) recorded less overlap, males in sub-groups of three males
together (MMM) recorded an increased of main range overlap at no food related to the other
two food levels (see Table I). Also Norbury et al. (in press) reported that on their study sites
feral ferrets and feral cats (Felis catus) moved significantly shorter distances in an area where
the prey population (rabbits, Oryctolagus cuniculus) had been reduced by only 77%,
compared with an area where the rabbit population was reduced by 99%. Similarly, cats on
the site where the rabbit population was reduced by only 77% had smaller home ranges than
at the same site before reduction of the prey population. The significantly greater proportion
of mobile ferrets observed at Norbury’s 99%-reduction site and in our study (MMM) (Table I)
suggests that the ‘low threshold’ in Fig. 6 had been reached and that intrasexual territoriality
was breaking down.

In a high density population of feral ferrets, males exhibited up to 9.2% overlap and up to
3.8% and 7.8% more overlap between the sexes than between the males or females
respectively (Ragg in review). Analysis of Norbury et al.’s. (in review) data shows that their
mean percentages of overlap of minimum convex polygons between the sexes (30.1%) was
significantly (ANOVA; $F_{2,15}=4.3$, $P=0.03$) larger than between male ferrets (25%) or female
ferrets (23%). This suggests that both populations were just below the ‘high threshold’, but
that intrasexual territoriality was still occurring.

A marten population with 5.9% male-male, 10.9% female-female and 37.1%-71.4% male-
female overlap (Katnik et al. 1994) may have been situated between the two thresholds. This
relationship between density and intrasexual territoriality has been also suggested for densely
stocked populations of bobcats (Lynx rufus floridanus) (Griffith & Fendley 1986), which
develop strong intrasexual territoriality at saturation densities (Fendley & Buie 1986). An
increase of food resources in western France in summer and autumn also coincided with increased intrasexual territoriality among European polecats (*Mustela putorius*), but during the low prey availability season, segregation between polecats increased (Lodé 1996). Similarly, the annual home range size of a lynx (*Lynx lynx*) population was smallest during the year of prey (hare) decline and largest in the second full year of prey scarcity (Poole 1994).

Therefore, as in other mustelids and carnivores (Erlinge 1974, Hornocker et al. 1983, Debrot & Mermod 1983, Ward & Krebs 1985, Griffith & Fendley 1986, Sandell 1989, Knick 1990, Brzezinski et al. 1992, Powell 1994, Lodé 1996, Alterio in review), food availability during the non-mating period and females’ spatial behaviour and availability during the mating period are likely to have been the primary determinant of variation in males’ main range size and variation in intrasexual territoriality for the ferrets in this study.
Figure 6. Proposed model of variation in intrasexual territoriality among solitary, sexually dimorphic carnivores during the non-mating period. Bold arrows indicate direction of the increase. Between the two thresholds there is reduced variation in females' home range size and territoriality.
Intrasexual territoriality and females’ tactics

Our results could not directly test Powell’s (1993) hypotheses that intrasexual territoriality is imposed on females by males. However, our results support the idea that females in small sexually dimorphic carnivour species exhibit intrasexual territoriality because of the high cost of maintaining exclusive individual territories. For these females, food is the most important resource so they should follow a behavioural tactic that maximises their chance of securing food resources to enhance reproduction and survival (Bailey 1974, Debrot & Mermod 1983, Sandell 1989, Lodé 1996). Therefore, when food levels increase and range overlap with males intensifies the best strategy for females in a population that lies between the thresholds (Fig. 6) is to maintain their territories to reduce competition with other females, but to show increased tolerance toward males (see Table I). In this study food variation did affect females’ spatial behaviour, but to a lesser extent than for males. Furthermore in this study when food levels increased and the males’ territories shifted from being relatively exclusive to being intrasexually territorial, females increased the territoriality toward other females. Conversely when food resources became scarce, females increased their territoriality (i.e. reduced amount of overlap) toward males.

Other studies have also recorded exclusive females territoriality toward males, and observed that this intolerance varies according to the season and resource availability. For example, in least weasels (*Mustela nivalis*), females have small home ranges within large male ranges; the females’ ranges are seldom contiguous and are used exclusively by the resident females Lockie (1966). Similarly during the non-mating period male stoats (*Mustela erminea*) can seldom enter female territories, even though the female’s territory may lie completely within his own (Erlinge 1974, 1977). Brzezinski et al. (1992) recorded that among polecats (*Mustela putorius*) the home range of females were mutually exclusive, yet sometime lay completely
within a male’s home range. Lodé (1996) concluded that increased of tolerance between polecats coincided with the increase in food resources during summer and autumn in western France. Female minks (*Mustela vison*) defend their territory against males even though male ranges could encompass one or more female territories (Lockie 1966, Gerell 1970).

**Implications for control operations**

This study has revealed that captive feral ferrets’ social structure and spatial behaviour during the non-mating and mating periods are affected by food availability, population density, social status and female abundance, so outcomes of control operations of feral ferrets are likely to differ depending on the reproductive status of the population. As spacing of control stations is determined by home range size, which in turn is influenced by variation in territoriality, the spacing between control stations will need to changed in response to variation in feral ferret territoriality (as discussed by Moller & Alterio in review). Furthermore, if the goal of the control operation is to reduce the numbers of breeders in the target population, control operations will be most effective in the non-mating period when reproductive females are socially dominant (Lodé 1996) and the home ranges of dominant males are smallest (Brzezinski et al. 1992, Powell 1994, Lodé 1996). Despite newly available adjacent territories and the low female density following a ferret control operation, established males that survive may benefit from remaining within their established territory if it provides a known distribution of potential mates and reduced competition with consexuals for food (Katnik et al. 1994). Therefore, an immediate second control operation in the same area early in the next non-mating period could be an effective way to target dominant resident male survivors and newly established females. Furthermore, the proposed model implies that it will be best to reduce prey density together with the predator density, so as to maintain the
territorial behaviour of carnivores between the thresholds. This should avoid the breakdown of intrasexual territoriality into undetermined spatial structure. As spacing of control stations is determined by the home range size (Moller & Alterio in review), undetermined spatial structure of the predator population will mean that the control stations may no longer be targeting the entire resident breeding population, nor the additional individuals that may now be dispersing.

Captive trials of the type reported here are useful for erecting new models and developing hypothesis, but need testing in the field. Therefore, we encourage future field studies on New Zealand ferrets that incorporate at least three similar areas with large numbers of resident feral ferrets. Each of these areas should have at least two study sites. The removal of ferrets from two sites of the first area, the partial removal of a known proportion of rabbits after the removal of a similar number of resident ferrets from two sites of the second area, and the use of two sites of a third area as experimental control, would be an effective way to test our predictions.

ACKNOWLEDGMENTS

We are grateful to the Department of Entomology and Animal Ecology, Lincoln University, for providing research facilities and funding. We also are grateful to the New Zealand Ministry of Foreign Affairs and Trade for the NZODA Postgraduate Full Scholarship that supported Gonzalo Medina-Vogel's studies. Dr. Chris Frampton provided excellent statistical advice.
REFERENCES

Alterio, N. In review. Spring home range, spatial organisation and activity of stoats *Mustela erminea* in a South Island *Nothofagus* forest, New Zealand. *Ecography*.


81


The effect of food availability and mating period on the behaviour and activity levels of captive feral ferrets

*(Mustela furo L.)*

GONZALO MEDINA-VOGEL*, GRAHAM J. HICKLING* & B. KAY CLAPPERTON**

*Department of Entomology and Animal Ecology, P.O. Box 84, Lincoln University, Canterbury, New Zealand.

**49 Margaret Avenue, Havelock North, New Zealand.

Paper prepared for Animal Behaviour

Abstract. We observed eight male and five female captive feral ferrets (*Mustela furo*) directly and by video camera in an outdoor enclosure consisting of a 36 m² arena and six dens and 13 tunnels. We assessed the effect of food availability, mating period, social status, density and group composition on the ferrets' behaviour (resting, grooming, vigilance, feeding, moving, aggressive interactions, marking and mating) and daily activity level. From May 1995 to December 1996, five (Replicate I) and six (Replicate II) social groups were tested. On average ferrets spent 86% of their time resting, 6% foraging and 3% vigilant. Dominant males rested more than did subordinate males. Ferrets with food in excess of their maintenance requirements spent more time resting than did ferrets with maintenance food or
no food. During the non-mating period males concentrated their activity between 0900 h and 2055 h whereas females were most active between 1500 h and 2055 h. During the mating period, females rested less, interacted less and mated more than males. Dominant males rested less, marked more and mated more than subordinate males. During the mating period dominant males and females concentrated their activity between 1500 h and 0855 h. When ferret density increased, individual ferrets concentrated their activity between 1500 h and 2055 h during the non-mating period and between 1500 h and 0855 h during the mating period. Variation in food availability affected the ferrets' activity level only during the non-mating period. These results are discussed with reference to the observations reported in Chapters four and five, and previous studies of mustelids in the wild.

*Behaviour and activity levels of Mustela furo*

Little is known about wild ferrets' behaviour and activity levels in relation to food availability and the mating period (see Blandford 1987 for a review), but relevant observations have been made on related mustelid species. Blandford (1987) described polecats (*Mustela putorius*) as being predominantly nocturnal, with crepuscular activity peaks, although there are many reports of polecats also foraging during the day. Polecats' activity was correlated with that of their prey and modified by the weather. In a study of stoats (*Mustela erminea*) in Sweden, Erlinge (1979) reported that one male was more active by night in winter than another in spring, or a third in autumn. He attributed these differences to the transient behaviour of juveniles, which have a tendency to be active during the day (Debrot et al. 1985). Male stoats exhibit intensive activity in autumn due to a modification in the spacing pattern of the population, but females remain less active until the end of autumn (Erlinge 1977, Debrot et al.
Erlinge (1977, 1979) emphasised that the increase in activity was affected by sex-specific seasonal changes in the day-night rhythm. Erlinge (1979) also concluded that as stoats can hunt voles (*Microtus agrestis*) when they are resting in their tunnels, their hunting was independent of the activity rhythm of the voles. Gerell (1969), in southern Sweden, found that male mink (*Mustela vison*) were mainly nocturnal in all seasons, with the level of activity increasing in winter (when nights were long and temperatures low). Similarly Gerell (1969) found that the peak activity of male mink coincided with peaks in prey activity. Linn & Birks (1980), in England, found that mink could be either nocturnal or active both night and day, but were never exclusively diurnal.

Our studies to determine spatial behaviour of ferrets in captivity (see Chapters 3, and 4) provided an opportunity to observe the behaviours of male and female ferrets. The aim of the work reported in this chapter was to determine the effect of variation in food availability and the mating period on the ferrets' behaviours and activity level, to contribute to the understanding of the behavioural ecology of feral ferrets under New Zealand conditions. Dispersal was considered an important behaviour of ferrets during periods of reduction in food availability (Chapter 4), as was the difference in main range size and overlap between ferrets of different social status determined before and during the mating period (Chapter 4). Interpretation of these observations will be aided by an understanding of variations in activity between ferrets.
METHODS

Outdoor enclosure

We constructed an experimental enclosure consisting of a 36 m² arena and six den boxes, each with one transparent wall and connected to the enclosure by tunnels (see Fig. 1, Chapter 3). Each den box had two gates, one to close the tunnel and the other to remove or introduce the ferrets without the need to enter the enclosure. Ferrets not currently in experimental use were kept in separate cages (see Chapter 3).

General procedures

We conducted seven trials during the non-mating period (May to July 1995) and 14 trials during the mating period (July 1995 to January 1996) (termed Replicate I). A further 15 trials during the non-mating period (May to September 1996) and 12 trials during the mating period (September to December 1996) (termed Replicate II), with different ferrets in each replicate. The start of the mating period was indicated by increased abdominal scent marking and body contact between males and females, and confirmed by later observations of copulation (cf. Poole 1967, Clapperton 1989, Grant & Hawley 1991). Replicate I consisted of five social groups and Replicate II of six social groups; a 'social group' was defined as a group of ferrets (i.e., ferret alone, two males, two females, one male with two females, two males with one female, or three males) placed in the enclosure for a trial. Ferrets in each social group were tested with three levels of food availability (termed 'no food', 'maintenance', 'double maintenance'). After capture from the wild, each ferret was kept in a separate cage for at least seven days to habituate it to the food (rabbit meat and commercial cat food) and cage conditions. Each was then kept alone for a 3-day acclimatisation period in the outdoor enclosure. After every trial we removed each ferret from the enclosure and returned it to its cage until the next trial. We also removed all
scats from the enclosure and dens and washed the dens and their tunnels with water.

During each trial of Replicate I and II, we recorded each ferret using a video camera for 24-h (one day) supplemented with sporadic direct observations at each level of food availability.

Ferrets received a 'maintenance' level of food throughout the acclimatisation period and while in individual cages. This consisted of 100 g of commercial cat food and/or rabbit meat per day, which maintained adult ferrets at constant body weight (Medina-Vogel pers. obs.). Food was provided daily by scattering it randomly in the enclosure; maintenance food was provided between 0600 and 0700 in the morning and between 2200 and 2300 in the night, double maintenance food was provided five times a day, beginning between 0600 and 0700 and ending at 2300 hours.

All ferrets used (two females and three males in Replicate I; three females and five males in Replicate II) were trapped near Christchurch at the beginning or during each replicate. Two females (Replicate I) and two males (Replicate II) were juveniles at the time of capture. Each ferret was individually marked with a coloured collar (black, red or white) and ear tag (right ear, left ear, or none).

Behaviours and activity level

We determined captive feral ferrets' behaviours by scoring at 5-min intervals each activity by the video camera in the enclosure, using a standard set of behaviour categories (some of which had subcategories). Each ferret observed was classified as resting, grooming, vigilant, foraging (feeding and searching for food), interacting (offensive, defensive, avoiding, submissive), marking (scent marking, faecal marking, smelling), moving (moving from one point to another inside the enclosure) and mating (courting and copulating) (after Poole 1967; Erlinge 1977, Shimek & Monk 1977, Estes et al. 1982, Clapperton 1989). The extent of each
behaviour was calculated by dividing the total time that each behaviour was recorded by 288 (i.e., the number of 5-min intervals in 24-h). Activity levels were derived by calculating the total time invested in each of the described behaviours (excluding resting) over each of four 6-hours periods (randomly chosen to be 0900 - 1455, 1500 - 2055, 2100 - 0255 and 0300 - 0855) divided by 72 (i.e., the numbers of 5-min intervals in 6-h).

Each male and female ferret’s social status was assessed by evaluating its offensive, defensive, avoidance and submissive reactions (Poole 1967, Erlinge 1977). Ferrets that exhibited offensive reactions, were frequently aggressive toward others, and won fights in all groups tested were considered dominant. Those that showed flank shielding or refused to fight (by immediately adopting a defensive posture towards the approaching aggressor) were considered subordinate (after Poole 1967).

Statistical analysis

The complicated nature of the main effects and interactions being tested in this study and the impossibility of testing several hundred independent combinations of animals, meant that most effects were replicated and tested as between and within animals effects. For example, most animals were tested in mating and non-mating periods under three feeding regimes, but no ferrets could be included within all social group types and not all ferrets experienced both types of social status. Additionally, the limitations on the number of combinations meant that many higher order interactions could not be evaluated. The data were analysed using SYSTAT’s General Linear Model option for unbalanced designs (MGLH; Kirby 1993), in which all effects and estimable interactions were entered. Individual ferrets, or ferrets’ social groups, were also included in the model as ‘blocking’ effects. The significance between categories within each factor (i.e. behaviours and time blocks) was assessed pairwise using
Fisher's Least-Significant-Difference test (LSD). Significance was set at $P<0.05$ throughout, and all proportional data were arcsin-transformed before analysis. Standard errors (SE) rather than standard deviation (SD) are given, as the focus of the analysis was on the significance of the different variables between the various treatments.

**RESULTS**

**Time budgets**

On average, captive feral ferrets spent $86\pm5\%$ (SE) of their time resting, $6\pm5\%$ foraging and $3\pm5\%$ vigilant. During the mating period, males spent $85\pm0.5\%$ of their time resting, $5\pm0.5\%$ foraging and $2.6\pm0.4\%$ mating, whereas females spent $81\pm1\%$ resting, $1.7\pm1\%$ interacting and $6\pm1\%$ mating (Fig. 1). Male spent more time foraging than did females ($F_{1,197}=5.3, P<0.02$). During the mating period ferrets spent significantly more time vigilant ($F_{1,197}=5.0, P<0.03$), moving ($F_{1,197}=8.8, P<0.01$) and interacting ($F_{1,197}=12.1, P<0.01$) than in the non-mating season. Dominant male were more vigilant ($F_{1,197}=7.5, P<0.03$), moved more ($F_{1,197}=8.9, P<0.01$) and interacted more ($F_{1,197}=13.0, P<0.01$) than subordinates ferrets. Furthermore, it was only the dominant male ferrets that increased their time spent vigilant ($F_{1,197}=7.5, P<0.01$), moving ($F_{1,197}=8.9, P<0.01$) and interacting ($F_{1,197}=13.0, P<0.01$) during the mating period.

Variation in density and food also significantly affected the time budget. Three ferrets inside the enclosure rested significantly more ($F_{8,197}=2.0, P<0.05$) at the no food level than did one or two ferrets. Variation in food availability affected the ferrets' time budget, but the effect differed between the mating and non-mating periods. Ferrets rested less ($F_{8,197}=2.0, P<0.05$) at maintenance and no food level during the mating period because they were
spending more time vigilant \((F_{2.197}=4.5, P<0.01)\), foraging \((F_{2.197}=3.7, P<0.03)\) and moving \((F_{2.197}=4.2, P<0.02)\) (Fig. 2).

**Activity levels**

Activity level differed significantly \((F_{1.900}=4.9, P<0.03)\) between the non-mating and mating periods (Fig. 3). In contrast to the non-mating period, both male and female ferrets significantly intensified their activity between 2100 h and 0855 h (Fig. 3).

Dominant male ferrets were significantly \((F_{1.900}=9.2, P<0.01)\) more active from 1500-0855 h, whereas subordinates exhibited no significant difference in activity between periods. Females also concentrated their activity from 1500-0855 h. No differences in activity level in relation to their social status were apparent.

There was also a significant effect of social grouping \((F_{4.900}=7.4, P<0.01)\) on activity levels. During the mating period, two males with one female ferret spent significantly less time resting, and concentrated more of their activity between 1500 h and 0855 h, than did two males or three males (Table I). In contrast, during the non-mating period three males together concentrated significantly more of their activity between 0900 h and 2055 h than did two males or two males with one female (Table I).

There was a significant \((F_{2.900}=4.9, P<0.01)\) effect of food availability on the activity level of captive ferrets. Ferret receiving food maintenance and no food concentrated their activity significantly more (Fisher's LSD; \(P<0.05\)) in period one (0900-1455) than when receiving no food.
Figure 1. Arcsin-transformed proportions of time (excluding resting) spent by eight male and five female ferrets during the a) non-mating and b) mating periods. Numbers indicate the number of times that behaviours were recorded, error bars indicate ± SE. Behaviours with different letter subscripts within each sex occurred at significantly different rates (Fisher’s LSD: $P<0.05$).
Figure 2. Variation in the arcsin-transformed proportions of time (excluding resting) of eight male and five female ferrets at three food levels (DFM: double maintenance food, FM: food maintenance and NF: no food) during the a) non-mating and b) mating periods. Numbers indicate the number of times that behaviours were recorded, sample size, error bars indicate ± SE.
Figure 3. Activity level of eight males and five female ferrets during the a) non-mating and b) mating periods. Numbers indicate the number of time that the activity levels were recorded, error bars indicate ± SE. Between and within sexes blocks of hours with different letters are significantly different (Fisher’s LSD: $P<0.05$).
Table I. Comparison of the activity levels (expressed as proportions of time observed) of three sub-groups of ferrets during the non-mating and mating periods \((MMF: \text{two males and one female, } MM: \text{two males, } MMM: \text{three males})\). \((N)\): Number of time that the activity levels were recorded, \((F)\): frequency, \((SE)\): ± standard error. Within each period, groups with different letters differ significantly in their activity (Fisher’s LSD: \(P<0.05\)). \(P\) indicates the overall significance of the difference of time activity levels between groups.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Non-mating activity level</th>
<th>Mating activity level</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(N)</td>
<td>(MMF)</td>
</tr>
<tr>
<td></td>
<td>(F)</td>
<td>(SE)</td>
</tr>
<tr>
<td>0900-1455</td>
<td>66</td>
<td>0.14</td>
</tr>
<tr>
<td>1500-2055</td>
<td>66</td>
<td>0.22</td>
</tr>
<tr>
<td>2100-0255</td>
<td>66</td>
<td>0.07</td>
</tr>
<tr>
<td>0300-0855</td>
<td>66</td>
<td>0.11</td>
</tr>
</tbody>
</table>
DISCUSSION

Time budgets

Captive ferrets spent on average 14% of their time active during the non-mating period (May to July), compared with 16% to 19% during the mating period (July to January). These levels are somewhat lower than observed in mustelids such as stoats (*Mustela erminea*, 25% to 34%) in Sweden, sea otter (*Enhydra lutris*, 5% to 91%) in California, marine otter (*Lutra felina*, 30% to 45%) in southern Chile, and mink (*Mustela vison*, 14% to 42%) in southern Sweden (Gerell 1970, Shimek & Monk 1977, Erlinge 1979, Estes et al. 1986, Medina 1993). Activity was presumably lower for these captive ferrets because of the artificial limitation to their movements. The artificial feeding situation meant that time spent moving from one hunting site to another, and time spent hunting, were reduced in relation to free-ranging mustelids. As in the wild, captive ferrets spent most of their active time foraging (Gerell 1970, Shimek & Monk 1977, Erlinge 1979, Estes et al. 1986, Medina 1993), and during the mating period increased their foraging, interacting, marking and mating rates (cf. MacLennan & Bailey 1969, Erlinge 1977, Grant & Hawley 1991). On several occasions females were observed hiding food inside the tunnels; as it was not possible to observe ferrets inside the tunnels, any time spent eating would have been classified as resting time. Therefore, the resting period may have been slightly overestimated and the feeding time underestimated.

Subordinate males spent more time active than did dominant males during the non-mating period, which is the same pattern as seen in juvenile stoats (Debrot et al. 1985). However main range of subordinate males were smaller than that of adults (see Fig. 4 of Chapter 4). Therefore, between ferrets of different social status this behaviour is probably associated with dispersal; it is likely that subordinate male ferrets were trying to stay peripheral to the dominant male’s territory (cf. Erlinge 1977, Woollard & Harris 1990).
The amount of time spent active by mustelids has been shown to be correlated with the extent of their movements, particularly for males in spring and summer (Gerell 1969, 1970, Erlinge 1974, 1977, 1979, Debrot & Mermod 1983, Hornocker et al. 1983, Sandell 1986, Debrot et al. 1985, Arthur et al. 1989, Brezezinski 1992). In our study, ferrets were most active during the mating period (spring) than the non-mating period which coincided with the period when females and dominant male's main ranges were largest (see Fig. 2, 4 of Chapter 4).

Contrary to observations by Gerell (1969) and Erlinge (1979), in our study food availability affected the time budget of the ferrets: During the non-mating period ferrets rested more when in food availability was high; during the mating period ferrets were more active and mated more when food was at maintenance than when it was either more or less abundant.

Activity levels

During the mating period, our study clearly showed that the activity level of the captive ferrets was affected by social status and the presence of females, but not by food availability. This supports Erlinge's (1979) observations that stoat hunting patterns are independent of the activity rhythm of their prey. However, contrary to Erlinge's observations, food availability did affect ferrets' activity level during the non-mating period. Ferrets at the food maintenance and no food levels concentrated their activity close to the first feeding time in the morning, whereas when food was being distributed five time a day (i.e. double maintenance) they did not show any tendency to concentrate their activity in any of the four 6-h periods.

Erlinge & Sandell (1986) have proposed that in intrasexual territorial mustelids, the males' territorial behaviour breaks down during the mating period because they adopt a roaming strategy that will give them opportunities to mate with several females. Our observations
support this, as it was only the dominant male ferrets that varied their activity level to correspond with that of the females (Table II, Fig. 4); these dominant males also increased their main range and movements (see Fig. 4 of Chapter 4). However, contrary to Erlinge and Sandell's observations our subordinate male ferrets did not attempt to be constantly in contact with the female. This was probably because the limited space of the enclosure artificially increased the likelihood of then encountering the dominant male. Consequently, the small main range and area overlap of subordinate males recorded during the mating period (see Fig. 4 and Table II of Chapter 4) was probably an avoidance strategy adopted in response to the continuous presence of a dominant male. Similarly, the small main range and area overlap evident during the no food level trials (see Table I of Chapter 4) probably represent an avoidance strategy adopted to minimise aggressive interactions and competition; in the wild, such behaviours are likely to promote dispersal (see Chapter 4).

Food availability and season both affected activity levels and time budgets; and the responses of captive ferrets to these effects varied between sexes, social status and ferret density. Consequently, this study suggests that in the field the results of monitoring campaigns from day or night trapping, radio tracking or direct observation may be influenced by both activity levels and by time budgets, which in turn depend on the season, time of the day, ferret density, social grouping and food availability. Therefore, monitoring, behavioural observations and radio tracking studies should be carefully planned to take into account diurnal and seasonal changes in the activity and time budgets of the ferret populations.
ACKNOWLEDGMENTS

We are grateful to the Department of Entomology and Animal Ecology, Lincoln University, for providing research facilities and funding. We also are grateful to the New Zealand Ministry of Foreign Affairs and Trade for the NZODA Postgraduate Full Scholarship that supported Gonzalo Medina-Vogel's studies. Dr. Chris Frampton provided excellent statistical advice.

REFERENCES


Spatial organisation of New Zealand feral ferrets

Studies on the spatial organisation of free-ranging feral ferrets in New Zealand have tended to be contradictory. Moors & Lavers (1981) in their mark-recapture study noticed that male and female ranges overlap extensively but that ferrets of the same sex are excluded from at least the centre of each ferret's home range. Home ranges of male ferrets averaged 31.3±18.6 ha and that of females 12.4±9.6 ha. They also observed that female ranges overlapped considerably when prey (*Mus musculus*) availability was high. In dry, tussock grassland habitat home ranges ranged in size from 111 ha for females to 288 ha for males (Pierce 1987). However, Ragg (in review a) noted that Moors & Lavers' (1981) estimates were based on trap locations, with few captures for some individuals, so it was not clear whether the home ranges in their study had been fully revealed. Consequently, there may have been more home range overlap than was apparent from the data presented. Ragg (in review a.) in Otago, New Zealand, recorded an average home range size of 85.6±9.6 ha for seven males, which was significantly larger than the average of 44.6±8.3 ha for 10 females. She also found an average percentage overlap of 9.2% between male-male pairs, 5.2% for female-female pairs, and 13% for male-female pairs. However, both Ragg (in review) and Norbury et al. (in review) have suggested that ferrets in New Zealand have higher rates of social contact than do other solitary mustelid species, and that the different conclusions of the various studies undertaken to date may be attributed to the different ferret density and spatial behaviour relative to prey density at the various study sites.
Norbury et al. (in review) in a tussock grassland habitat in New Zealand’s South Island recorded home ranges of 102±9.9 ha for 34 male ferrets and 76±9.1 ha for 28 females. The percentage of male home ranges that overlapped with other males ranged from 13-34% across sites. Female-female overlap was 11-23%, and overlap between the sexes was 12-31%. Norbury et al. (in review) supported Moors & Lavers’ (1981) conclusion that female home ranges overlap considerably when the abundance of prey (in this case rabbits) is unusually high; consequently they did not find intrasexual territoriality amongst their ferrets. Norbury et al. (in review) also found that male ferrets’ core areas (27±1.5 ha) were significantly larger than those of females (16±1.5 ha), with significantly less overlap between core areas than between home ranges.

From the data summarised above, and in Chapter two it seems that ferrets experiencing abundant food may reach high population densities and may not exhibit intrasexual territoriality as proposed by Powell (1994). However, Ragg based her conclusions on the range overlap of only one adult male ferret and eight sub-adult or juveniles ferrets with radiocollars, plus trapping data and denning sharing observations. Furthermore, her study was done between February and July (the ferrets’ non-mating period), when most of the sub-adult and juveniles ferrets would have still been within their mother’s home range (cf. Moors & Lavers 1981, Lavers & Clapperton 1990). Since the available information about ferrets’ spatial behaviour in New Zealand mostly relates to movements patterns during only a part of the year, I conclude that there is currently insufficient field information to determine the extent to which ferrets exhibit intrasexual territoriality in New Zealand. Accounts of other species’ spatial behaviour in the international literature show that there can be considerable differences in carnivore social behaviour over time, study areas and between species (see Chapter 2). Therefore, discussions about variations of intrasexual territoriality should be
made by comparing the variation in territoriality among a large number of individuals and pairs of the same species within particular study sites during both the non-mating and mating period, rather than by making comparisons between species and sites (e.g., Katnik et al. 1994, Herrmann 1994).

**Wild studies versus captive studies**

As was noted previously, relatively little is known about ferret ecology, movements and social behaviour in New Zealand, yet this information is critical to understanding the effect of ferrets in limiting rabbit numbers, their role in the epidemiology of Tb, and in designing effective predator control programme (King & Moors 1979; Moller et al. 1996; Ragg in review a). This lack of information about ferrets’ spatial behaviour is due in part to the difficulties and cost of studies to determine spatial patterns and behaviour of free-ranging animals (Harris et al. 1990). Of six radio-tracking and trapping studies of ferrets in New Zealand described by Moller et al. (1996), in all but one the sample size was small, the methods of estimation variable, and the number of fixes insufficient to have fully described some home ranges. Furthermore, several of these studies relied on live-trapping or denning for most fixes, which may severely underestimate their home range (Moller et al. 1996; Ragg in review a). Given this background, I chose to obtain information about the social and spatial behaviour of feral ferrets using an experimental captive-animal methodology. By comparing the results of this study with field research, I aimed to obtain reliable data that would help support or reject predictions and hypotheses about the mechanisms underlying variation in the territorial system of small carnivores and in particular feral ferrets in New Zealand.

The method developed in this study gave a realistic relationship between main range and core area sizes and variations among males and sexes, grouping and social status (see Chapter
3). True expansion of home range size, and dispersal, were obviously not possible for the ferrets in my experimental enclosure. Nevertheless, the methodology was able to demonstrate that an increase in food availability was associated with an increase in main range ‘size’, as seen in various field studies of mustelids (see Chapter 4). Furthermore, when food was scarce ferrets reduced their activity to core areas as an avoidance strategy.

One weakness of the methodology presented here is the sample size. It would have been preferable for the enclosure to have been at least 165 m² in area and equipped with 12 dens and several tunnels of different diameters. In such an enclosure it would have been possible to observe groups consisting of three females and two males, and to test during each period three such groups to obtain a total sample of 30 ferrets in a two year study. This would have allowed me to study the effect of food availability, density, social status and mating period separately, without needing to change social groups. Differences in tunnel diameter could have provided refuges for the smallest individuals.

If the size of the enclosure and the number of animals in the study were to be increased in future studies, it would become more difficult to observe them with video cameras. Therefore, the observation of ferrets inside a bigger enclosure might have to be by direct observation, perhaps supplemented with video recording of their activity inside dens. The use of transparent tunnels would help in the assessment of feeding and avoidance behaviours. A proven observation method in the field is scan sampling every 10 min (Estes et al. 1982, Ostfeld et al. 1982, Medina 1993), and this method could be applied in future captive studies.

It is also important to emphasise that captive studies need to be supported by field research. The type of captive study reported in this thesis has proven useful for erecting models, and raising new questions to be tested in the field. One suggestion for a suitable field study design was discussed in Chapter 4.
Models of intrasexual territoriality

Powell’s model

Powell (1993, 1994) proposed that some forest carnivores exhibit intrasexual territoriality because the distribution and availability of the most likely limiting resource for these species (food) allows a trade-off not possible for species with individual territories. Male spacing is consequently affected by female spacing, as well as by the distribution of food. Powell predicted that as prey populations vary from very low to very high densities, populations of solitary, sexually dimorphic carnivores will change their use of space in the following sequence:

transient → individual territories → intrasexual territories → extensive home range overlap

Powell (1993, 1994) could not identify a benefit that a female would gain from sharing a territory with a male; he therefore hypothesised that intrasexual territoriality in carnivores is imposed by males who are larger than, and thus dominant to, the females.

Refinements to the model

My study demonstrated that ferrets’ intrasexual territoriality varies with changes in food availability, as Powell’s model would predict. With an increase in food availability there was an increase in main range size and overlap. Conversely, when food was scarce the increase in aggressive interactions, which had the have potential to end in fights, instead resulted in increased avoidance behaviour. Since the ferrets could not disperse they instead restricted their activity to core areas to maintain territory and reduce range overlap. My results suggest that when food is scarce and male territoriality intense the best strategy for females in a
population between the thresholds (see Fig. 6 of Chapter 4) is to maintain intraspecific territories to reduce competition with other females, but to show tolerance towards males (see Table I of Chapter 4). In this study food variation did affect females' spatial behaviour, but to a lesser extent than for males. Furthermore in this study when food levels increased, and the males' territories shifted from being relatively exclusive to being intrasexually territorial, females increased their territoriality toward other females. Conversely, when food resources became scarce the females increased their territoriality (i.e. reduced their range overlap) toward males, and the males appeared to increase the exclusiveness of their territories toward boths other males and females (see Table I of Chapter 4).

My results thus supported Sandell's (1989) arguments that food is the most important resource for solitary females, which consequently adopt a behavioural tactic that maximises their chance of securing food resources (see also Bailey 1974, Debrot & Mermod 1983, Lodé 1996). The main difference of my model from that proposed by Powell (1993, 1994) is my hypothesis that food is the most important resource for both sexes during the non-mating period, and that the intrasexual territorial system will be influenced by individuals' social status, sex and predator density relative to prey density. Furthermore I predict that there is at least an indirect benefit for females to be intrasexually territorial, in that it may be too costly for them to do otherwise. My observations of the females in the enclosure suggested that they were physically capable of excluding the males, at least for short periods. However, given ferrets' sexual dimorphism (Lavers & Clapperton 1990) it is likely that there will be a high energetic cost, and risk, involved for females that attempt to do so throughout the year. For many females, it may be that there are insufficient corresponding benefits to be worth the cost of attempting to exclude the males from their ranges. Therefore, provided food resources are sufficient, it may be better for females to accept the males but to maintain their territoriality.
toward others females, as the dominant males will at least keep other males out (see Chapter 4). My model also takes into account that variation in spatial overlap is not a variation in territoriality *per se* but is a result of changes in the size of the respective ranges.

*The effect of the mating period*

During the mating period food and females are resources that are not equally important for male ferrets of different social status. When females were removed from the enclosure during the mating period, male ferrets increased their intrasexual territoriality, since a behaviour aimed at maximising the number of matings no longer had economic benefits for the dominant males. In this study females could not choose to leave the enclosure themselves, and there was only one dominant male with access to them, so females in oestrus were not a variable resource. Therefore, decreased intrasexual territoriality (i.e., more overlap) between the captive male ferrets when I removed females from the enclosure during the mating period seems likely to have been related to a change in male behaviour induced by the variability of the new critical resource (food), since exclusive territories to maximise access to mating were no longer useful. Erlinge and Sandell (1986) predicted this behaviour, and I have demonstrated that it mainly affects the dominant males.

*The model's predictions*

My model is based on the hypotheses that there are two thresholds, at low and high prey density levels, between which small carnivores will show intrasexual territoriality (see Fig. 6 of Chapter 4). As prey availability increases, subordinate males' home ranges will increase and consequently all individuals' area overlap will increase. Females' intrasexual territoriality will show little variation between the two thresholds. However, if prey
abundance falls below the low threshold, the intrasexual territoriality of males and females will break down and many will disperse. If prey availability exceeds the high threshold, I predict that there will again be a breakdown of intrasexual territoriality, however in this case only individuals of low social status will increase their home ranges, and females will try to avoid each other. In both cases, once intrasexual territoriality has broken down the spatial structure of the population will fluctuate unpredictably for an indeterminate period.

Management implications

This study has revealed that captive feral ferrets’ social structure and spatial behaviour during the non-mating and mating period are affected by food availability, population density, social status and female abundance, so outcomes of control operations of feral ferrets are likely to differ depending on the reproductive status of the population. If the goal of a control operation is to reduce the number of breeding ferrets in the target population, my findings suggest that control operations will be most effective during the non-mating period when there will be increased social dominance of reproductive females and the home range of dominant males are smallest. Despite the newly available adjacent territories and low female density after a control operation, well-established male feral ferrets that survive may benefit from remaining within their established territories, so that they retain access to a known distribution of potential mates. Therefore, a second control operation in the same area early in the next non-mating period to target dominant resident males and the newly established females should enhance the effectiveness of the control work.

According to my proposed model of variation in spatial and social behaviour of small carnivores (e.g. feral ferrets) with changes in food (prey) availability and predator density, it may be better to reduce prey density together with the predator density, so as to maintain the
territorial behaviour of carnivores between the thresholds. Ferret will maintain large home ranges and intrasexual territorial behaviour that will help prevent rapid immigration of new ferrets into the controlled area (see Fig. 6 of Chapter 4). Increased prey availability may induce a reduction in the surviving males’ home ranges which may then induce increased immigration of new ferrets into the area. The males, and newly established ferrets, may consequently be more trappable relative to females at this time.

Food and season affect both activity level and time budgets, and the responses of captive ferrets to these effects varied between sexes, social status, ferret density and season. Consequently, this study also suggests that results of monitoring campaigns from day or night trapping, radiotracking or observation in the field will all be affected by ferrets’ activity levels and time budgets, which in turn depend on the season, hour of the day, social grouping, ferret population density and food availability. Therefore, monitoring campaigns, behavioural observations and radiotracking studies should all be carefully planned to take into account information about the activity level and time budget of the local ferret population.
SPECIFIC CONCLUSIONS

The specific conclusions that I reach from this study are listed below:

1. Results from this captivity study are similar to previous studies of other free-ranging feral ferrets in New Zealand.

2. The captive methodology tested in this study is generally appropriate for investigating certain aspects of ferret social and spatial behaviour.

3. Population density affected the size of captive ferrets’ main range and their patterns of use intensity of core areas, but not their intrasexual territoriality.

4. Intrasexual territoriality in carnivores works at several levels and so needs to be described in terms of spatial overlap, use intensity and temporal territoriality.

5. Intrasexual territoriality and den sharing between captive ferrets is affected by sex, group structure and social status.

6. Intrasexual territoriality benefits both male and female ferrets, and appears to be maintained because of different strategies of exploitation of unequally distributed resources between the sexes. The same is probably true for other species of small carnivores.
7. Many of the results of this study are consistent with Powell’s (1993) model where, in a high prey density situation, extensive home range overlap in carnivores is expected and, when prey are scarce, reduced overlap or individual territories are predicted.

8. Avoidance to reduce competition and prevent fighting may be the main factor that induces the dispersal of carnivores after the reduction of available food.

9. Variation in range area overlap among intrasexual territorial carnivores seems to be a function of the size of the respective main ranges and core areas rather than a function of variation in territoriality.

10. I hypothesise that intrasexual territoriality arises between high’ and ‘low’ thresholds of prey and predator abundance. Male small carnivores should vary their territoriality with changes in food availability, whereas female small carnivores should maintain their intrasexual territoriality to reduce intrasexual competition.

11. Above the high threshold and below the low threshold, intrasexual territoriality breaks down and the spatial structure of the carnivore population become indeterminate.

12. Dominant and subordinate captive male ferrets altered their spatial activity during the mating period. Dominant male ferrets’ spatial activity became highly correlated with the females’ spatial activity, whereas subordinate males generally avoided both females and dominant males.
13. Captive ferrets' spatial activity was affected by food availability only during the non-
mating period.

14. Receptive females in this study were a very 'predictable' resource, so the observation of
increased area overlap between male ranges if the female was removed during the mating
period, and the increase in male ferret intrasexual territoriality during the mating period,
both support Erlinge and Sandell's (1989) and Sandell's (1989) hypotheses that a variable
or unpredictable resource will induce a change in male territorial behaviour.

15. Food availability affected the time budget and the activity level of captive ferrets, but only
during the non-mating period.

16. The activity level of captive male ferrets was affected by both social status and female
abundance during the mating period.

17. The small main range and area overlap of subordinate captive male ferrets recorded at
the no food level, and during the mating period, was an avoidance strategy that may
 correspond to increased dispersal in wild conditions.

18. To succeed in a ferret control campaign, the model predicts that it may be best to reduce
prey density together with the predator density so as to maintain the territorial behaviour
of ferrets between the thresholds.
19. If the goal of a ferret control campaign is to reduce the number of breeding individuals, then the campaign should be carried out only in the non-mating period when reproductive females tend to be more socially dominant.

20. Discussions about variation of intrasexual territoriality should emphasise comparisons among individuals and pairs of the same species within particular study sites. Special care is needed to avoid misinterpretations arising from the inclusion of transient or subordinates in such analysis.

REFERENCES

The following list includes all references cited in Chapters 1, 2 and 6.


Mammal Rev., 17, 155-198.


Erlinge, S. 1968. Territoriality of the otter Lutra lutra L. Oikos, 19, 81-98.


King, C. M. 1983. The relationship between beech (Nothofagus sp.) seedfall and population of mice (Mus musculus), and the demographic and dietary responses of stoats (Mustela erminea), in three New Zealand forests. J. Anim. Ecol., 52, 141-166.


